OILBIRDS OF VENEZUELA: ECOLOGY AND CONSERVATION

ROBERTO LUIS ROCA

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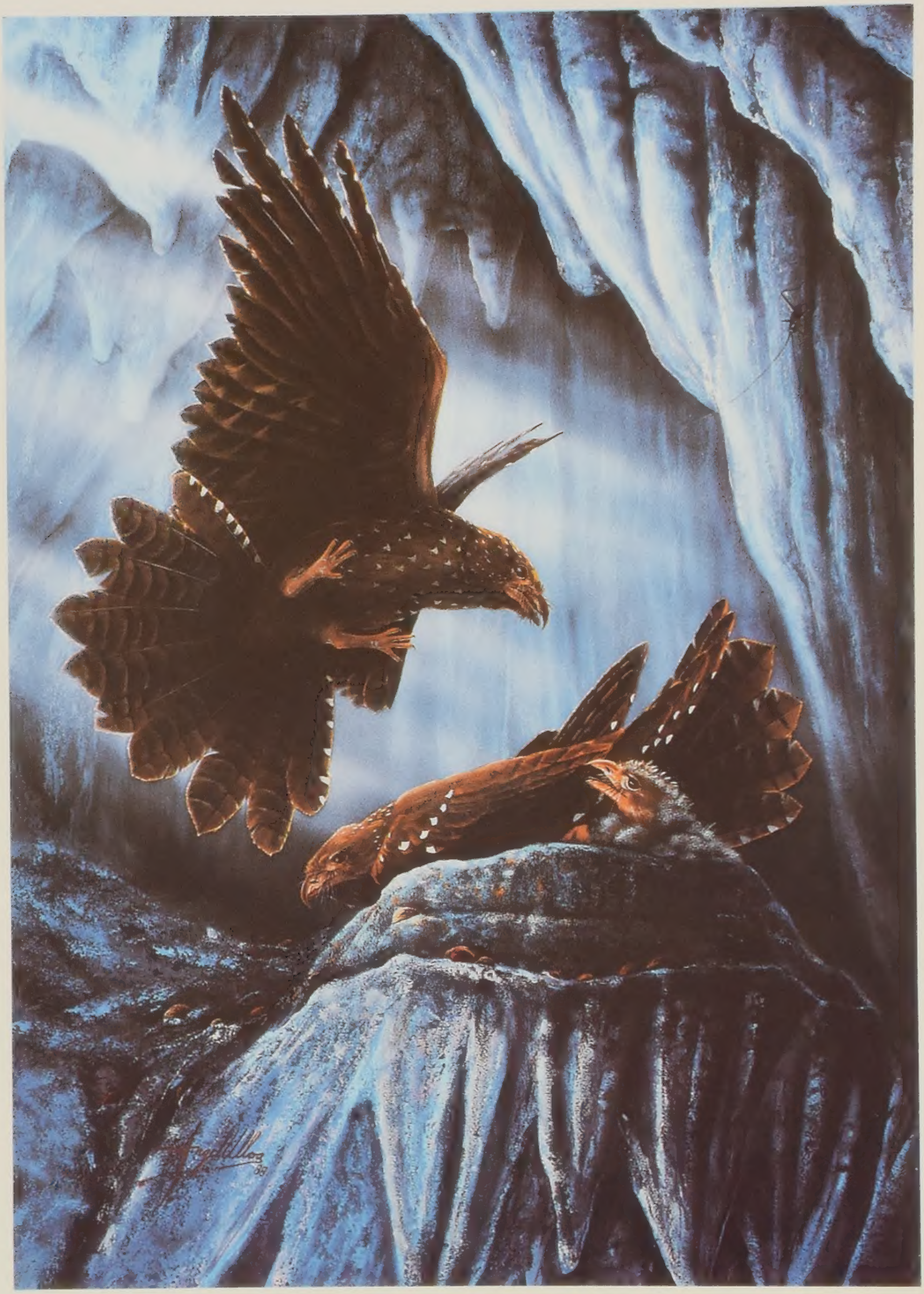

OILBIRD (*Steatornis caripensis*)
Painted by Angel Ulloa

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ROBERTO LUIS ROCA

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1

FORAGING ECOLOGY

Ecological and Evolutionary Context of Frugivory

Ecologists for decades have studied natural populations to test hypotheses about competition and predation and have developed theories to explain the way communities are structured in different environments (May, 1981; Pianka, 1982). Recently, through the development of behavioral ecology, optimal foraging theory has provided a conceptual framework toward understanding animal foraging tactics as a consequence of natural selection (Krebs and Davies, 1984). Partly by borrowing ideas from economists, ecologists have created optimal foraging models using fitness related cost/benefits derived from behavioral interactions of animals among themselves and with their resources (Krebs and Davies, 1984; Stephens and Krebs, 1986). Optimal foraging by frugivores is receiving increasingly more attention (Wheelwright, 1983; Moermond and Denslow, 1983, 1985; Levey, et al., 1984; Foster, 1987; Moermond, et al., 1987; Worthington, 1989). Connections between the natural history of frugivores and optimal foraging theory are still being developed.

Frugivorous birds have been examined from several ecological and evolutionary perspectives. The study of fruit and frugivorous birds is relatively recent and quantitative studies can be dated from the publications of Snow (1961, 1962, 1965, 1971). Snow suggested that long-term mutual interactions between plants and the birds that disperse their seeds could result in coevolving mutualistic systems; plants would benefit from seed dispersal and fruit-eating birds would gain from the fleshy pericarp of the fruit. The nature of the interaction, according to Snow, would promote interspecific competition among plants, in terms of fruiting times, in order to have more of their seeds dispersed by birds. Any species fruiting at a time when few other species were in fruit would have a selective advantage, and a temporal displacement in fruiting periods would be the most likely result. These selective processes could lead to the fairly continuous production of ripe fruit throughout the year in most tropical forests (Snow, 1971).

Moermond and Denslow (1985) have highlighted that an important ecological difference between fruit and insects as food sources lies in their relative availability to birds. Fruit-eating birds promote the reproduction and dispersal of their food plants, so natural selection presumably favors the evolution of abundance and accessibility of the fruit. On the other hand, bird predation on insects moves in the opposite direction. Selection operates to strengthen the predator-avoidance mechanisms and the crypticity of insects. The result of these selective processes may be that frugivorous birds spend less time and energy locating and handling fruit than they would if hunting for insects. Insectivorous birds, on the other hand, evolve complex behaviors and morphological adaptations to improve their efficiency as predators. Fruit-eating birds forage on "easy" prey that are sessile, nonelusive, relatively undefended (Snow, 1971), and do not require complicated searching and handling techniques (Snow, 1971; Moermond and Denslow, 1985).

Frugivorous birds face different constraints when foraging. Wheelwright (1985) showed that fruit size presumably could be an important trait used by plants to discriminate among birds that are potential dispersers of their seeds. Wheelwright found that fruit-eating birds with broad gapes consumed larger fruits, as expected, than narrow-gaped birds, but they also ate medium and small-sized fruits. The implication is that plants with larger fruits attract fewer birds than plants with small fruits. McKey (1975) hypothesized that some fruit traits, such as a highly nutritious pulp and fruit size, have evolved in response to the selective pressure of specialized frugivorous birds that provide successful seed dispersal of their food plants. An extreme mutualistic case is that of the Dodo (*Rhaphus cucullatus*) and its major food plant, *Calvaria major*. Following the dodo's extinction 300 years ago, *Calvaria* seeds have not germinated, apparently because they depended upon scarification during digestion by dodos (Temple, 1977). It should be noted, however, that this relationship has been disputed by Owadally (1979).

Current theory emphasizes caution in attributing plant and bird interactions as the result of coevolution (Wheelwright and Orians, 1982; Howe, 1982; Herrera, 1986). There are other potential selective factors acting on traits related to the dispersal process that could also influence plant reproductive strategies. For example, nonmutualistic frugivores that damage fruits and seeds, interspecific competition among coexisting plants, weather patterns, and topographic features all could influence the quality and availability of fruit (Herrera, 1986; Howe, 1982).

Perspective of the Frugivore

Morton (1973) studied the benefits and constraints associated with frugivory, as opposed to insectivory, by some tropical birds. He hypothesized that total frugivory should be rare because it results in lower growth rates than those allowed by animal food. Long development time would increase the risk of predation at the nest and that would counteract the benefits of exploiting abundant and accessible fruit. As a response to such selective pressures, various feeding strategies are expected to evolve in different bird species. As predicted, only a few tropical birds, such as Oilbirds (*Steatornis caripensis*) and Bearded Bellbirds (*Procnias averano*) eat only fruit as adults and nestlings (D. W. Snow, 1961, 1962; B. K. Snow, 1970; Moermond and Denslow, 1985). Most birds eat fruit, insects, and other invertebrates in varying proportions, and those that feed almost exclusively on fruit as adults usually feed insects to their young (Morton, 1973; Moermond and Denslow, 1985). There are other constraints related to foraging on fruit. In tropical forests, fruit availability fluctuates in both spatial and temporal dimensions; the fluctuations seem to be the result of environmental changes (Foster, 1982, 1985; Frankie, et al., 1974; Howe, 1982; Wheelwright, 1986). Even in tropical environments with few seasonal changes the relative abundance of various fruits changes throughout the year (Snow, 1965). These fluctuations influence the life histories of frugivorous birds. Some fruit-eating birds, such as the Yellow-green Vireo (*Vireo flavoviridis*), the Clay-colored Robin (*Turdus grayi*), and manakins (Pipridae), seem to have adjusted their breeding to fluctuations in fruit production. The initiation of breeding takes place only when fruit becomes abundant (Morton, 1973; Wheelwright, 1983; Worthington, 1982).

Birds that face the problem of food resources fluctuating within critical levels may shift to feeding on other resources, or they may move to another area where the original food is still available (Karr, 1976; Wheelwright, 1986). Additionally, frugivorous birds such as quetzals (*Pharomachrus* spp.), bellbirds (*Procnias* spp.), and toucanets (*Aulacorhynchus* spp. and *Selenidera* spp.) delay their breeding season during fruit shortages (Wheelwright, 1986). Some frugivorous birds respond to local shortages in fruit availability by increasing the time they spend foraging or by seasonally following their major food sources. Foster (1977) indicated that the Long-tailed Manakin (*Chiroxiphia linearis*) spent more time feeding and less time engaged in reproductive displays during periods of food shortages in Guanacaste, Costa Rica. Wheelwright (1983) reported that a population of Resplendent Quetzals (*Pharomachrus mocinno*) at Monteverde, Costa Rica, shifted as the fruiting seasons of some species of Lauraceae changed. Lauraceae comprised about 50% of the quetzal's diet and local dispersal of the quetzals correlated highly with phenology. Male Three-wattled Bellbirds (*Procnias tricarunculata*) rely mainly (60-80% of their diet) on lauraceous fruit when they engage in breeding displays on their perches. These birds responded to fluctuations in fruit availability by shifting to other lauraceous species when their fruit became more abundant (Wheelwright, 1986).

The way different frugivorous birds capitalize on their food resources is central to understanding both their foraging ecology and the evolution of their foraging strategies. The foraging behavior of frugivorous birds, as well as that of other animals, represents a response to conflicting ecological and evolutionary pressures (Hamilton and Watt, 1970; Schoener, 1971; Charnov, et al., 1976; Heithaus and Fleming, 1978). Frugivorous birds are under selective pressures to maximize their fitness. Their fruit-searching behavior should in some way at least balance the rate of energy and nutrient intake, and minimize the risk of predation. Frugivorous birds that inhabit tropical, seasonally variable environments must keep track of the presence or absence of ripe fruit in their foraging patches. They must leave their roosting place, travel to foraging patches, search for fruit, and handle it before ingesting it. According to the premises of the optimal foraging theory, those foraging activities that demand energy and time should follow an optimization process, maximizing net benefits, and ultimately resulting in a higher fitness for the foragers.

The foraging movements of tropical frugivorous birds are an important aspect of their foraging strategies, especially for frugivorous birds that are unable to stay on their current foraging grounds when resources decrease. The cost associated with the distance flown to reach their food plants, and the time they consume searching and foraging for ripe fruit, impose strong restrictions on the benefits obtained from these fruits. Additionally, the way they switch foraging patches must be a critical decision, especially because fruit patches are ephemeral, and sometimes are far from roosting and nesting places. Foraging movements of frugivorous birds are also important because they determine the quality of the dispersal services these birds render to their food plants. Such movements may change the spatial distribution and genetic structure of plant populations through the dispersal of seeds (Estrada and Fleming, 1986; Murray, 1986).

Little is known about the daily foraging movements of natural populations of frugivorous tropical birds and the Oilbird (*Steatornis caripensis*), the only completely nocturnal frugivore of the neotropics, has not been studied in this respect at all.

2

NATURAL HISTORY OF THE OILBIRD

The great naturalist and traveller, Alexander von Humboldt, discovered the Guácharo, or Oilbird, for science when he visited Caripe in northern Venezuela in 1799, but it was already known locally. "That which gives great celebrity to the valley of Caripe," he wrote, "is the great cavern of the Guácharos. In a country where people love the marvelous, an inexhaustible subject for conversation is afforded by a cavern that gives birth to a river and is inhabited by thousands of nocturnal birds the fat of which is used by the missions to prepare food" (Humboldt, 1817, as cited by Snow, 1976). Humboldt mentioned some of the other striking features of the Oilbird: how it leaves the caves at night to feed on the fruit of the forest trees, how its young become very fat, and how the birds make an indescribable clamor when they are disturbed in the caves. "The sharp and piercing sounds are reflected from the rocky vault and the echoes reverberate from the depths of the cavern" (Snow, 1976). The Guácharo attracted wide interest among zoologists during the 19th century because of its many peculiarities. Lacking close relatives, it was placed in the monospecific family Steatornithidae. *Steatornis* is somewhat similar in structure to members of the family Caprimulgidae (nighthawks and goatsuckers).

The Oilbird is a powerful and impressive bird, about 46 cm long, averaging 400 grams, and with a wing span of one meter. The beak is strong and hooked, hawk-like, and surrounded by stiff rictal bristles. The plumage is rich brown with sparse and conspicuous white spots on the wing coverts and outer wing and tail feathers. The legs are unfeathered and very short. The tail is long and when it is folded looks like an inverted V (Snow, 1961).

Oilbirds have low wing-loading (weight/wing area) and a very low aspect-ratio (wing span/mean width). These features enable them to fly slowly within caves. Oilbirds hover briefly in the air, back off, and circle around in agile flight in the vault of caves.

Well inside their caves, the birds' deafening cries are calls of alarm and communication. The exact meaning of their vocalizations is unknown. While in flight they utter staccato high-pitched clicks used for echolocation (Griffin, 1953; Konishi and Knudsen, 1979); the sound bouncing off the cave walls enables them to avoid collisions in the pitch blackness. The sound energy of their echolocation system ranges from 1 to 15 kilohertz, with a dominant frequency range of 1.5 to 2.5 kilohertz. The smallest object avoided by them is a disk 20 cm in diameter (Konishi and Knudsen, 1979).

Oilbirds roost all day in caves, leave them at dusk in search of fruit, and return before dawn. When feeding they hover before plucking off one fruit at a time from the food trees. Apparently they take turns in collecting fruit; while one dives down to the exposed canopy fruit, the rest wait while circling the tree. They pluck and swallow the fruit whole, later digesting the edible pericarp, and regurgitating the seed intact. They are able to carry large loads of bulky fruit from remote feeding areas. At night Oilbirds fly swiftly over the forest canopy, increasing their flying speed by holding their wings in a more sweptback fashion, reducing the wing area (Snow, 1961). I have observed small groups of three to five individuals foraging together on the same laurel. In Trinidad they forage on approximately 10 plant families and on at least 36 different species. Snow (1962) and Snow and Snow (1978) found that about 50% of the fruit consumed were palm fruit and most of the remaining diet consisted of fruit of species of Lauraceae and Burseraceae.

In 1961, 163 years after Humboldt described this species, Snow published a detailed account of the natural history of the Oilbird in Trinidad. Oilbirds are monogamous and share the duties of nesting. Snow assumed the pair–bond to be permanent. Both parents built a round nest, approximately 37 cm in diameter, made primarily of regurgitated fruit pulp and guano. Pairs maintain the same nest for several years. The nests are generally located on high ledges close to the cave ceiling. In Guácharo Cave these nesting ledges are up to 50 m high. On many ledges 10 to 40 pairs cram together, making it difficult to distinguish individual nests. A few ledges support solitary pairs (Roca and Gutiérrez, 1991). Pairs defend their small nesting area. When unestablished birds land near an occupied nest the resident pair utter loud, harsh calls. Sometimes they attack intruders, gripping them by the beak and twisting and pulling them.

The normal clutch is 2–4 eggs; the eggs are white. The average weight of a freshly-laid egg is 20.2 grams (Snow, 1961). The period between the laying of successive eggs varies between two and seven days. The eggs are incubated from the time they are laid, with both sexes incubating. The incubation period is 32 days. Both parents sit on the nest side by side brooding the eggs during the day but take turns at night. Pairs generally raise one brood a year. In Trinidad, with a less seasonal environment, some pairs raise up to two broods a year (Snow, 1961).

At Guácharo Cave egg laying begins between mid–March and early April, and most females are finished by early May. A few pairs may start late and produce clutches anytime during the breeding season, which usually extends through the beginning of September (Roca and Gutiérrez, 1991). By August and September thousands of fledglings fill Humboldt's Gallery.

Young Oilbirds at hatching weigh from 12 to 15.5 grams. The altricial nestlings hatch mostly naked and for about three weeks are unable to regulate their body temperature. After this time the new and abundant down feathers and the increasing fat deposits help control the body temperature. Nestlings remain in the nest until they are 95 to 120 days old. During that time they accumulate the great deposits of fat that have led to their being exploited for oil. At about 70 days the young weigh as much as 600 grams, considerably more than their parents. The young are fed at night on whole, undigested fruit during most of their development. Like the adults, the young digest the fruit pulp and regurgitate the seeds

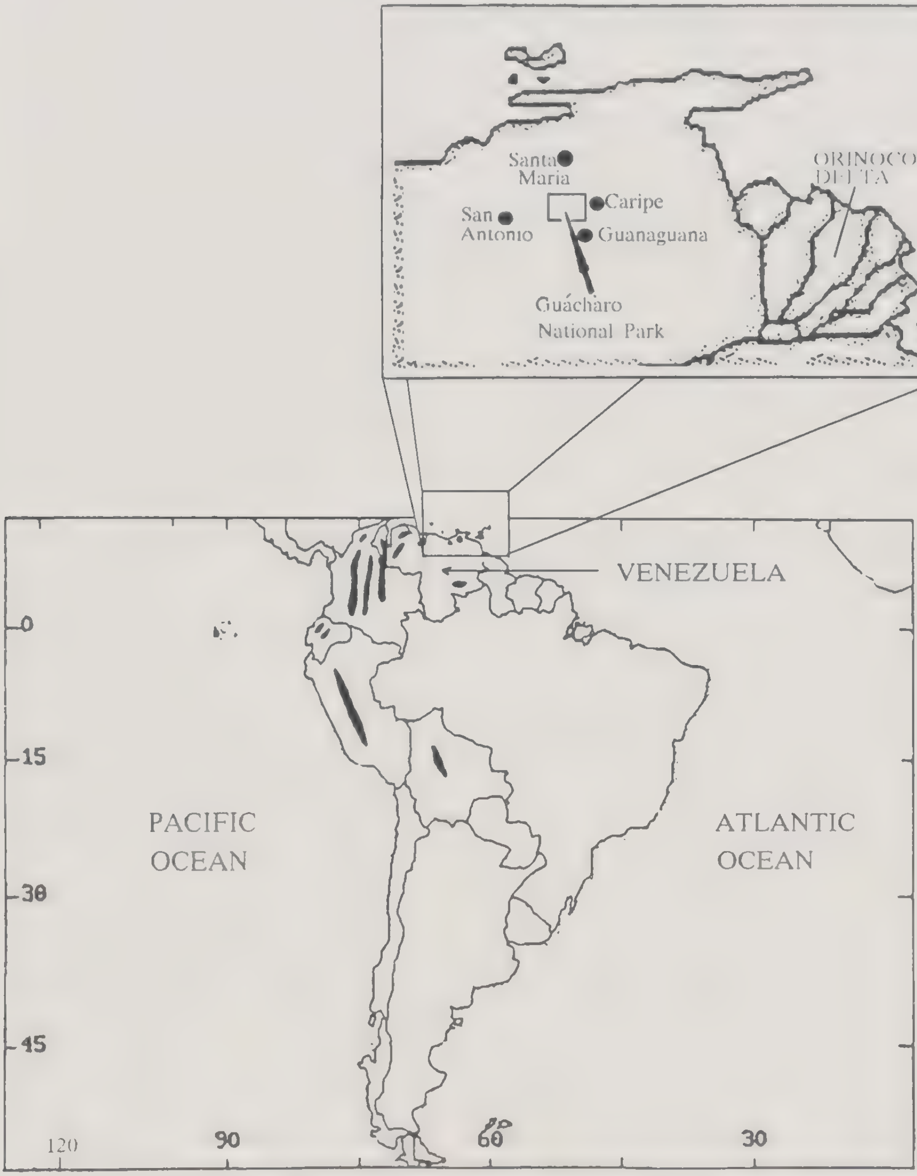


Fig. 1. Distribution (black) of Oilbird colonies in South America and the area of study. Field work was in Guácharo National Park in the Caripe mountains, Monagas and Sucre states, Venezuela.

(Snow, 1961, 1962).

The range of the Oilbird (Fig. 1) is northern and northwestern South America (Colombia, Venezuela, Trinidad, Ecuador, Peru, and Bolivia); there are three records from Panama (Ridgely and Gwynne, 1989:199) but its status there is uncertain. Despite its wide range, it is extremely vulnerable to human activities. Through both direct effects, such as the taking of nestlings, and indirect effects, such as habitat destruction, the Oilbird is suffering drastic reductions in numbers throughout its range. Snow (1962) reported the extinction of five of 13 known colonies in Trinidad. Bosque (1986) indicated that seven of 54 colonies in Venezuela have disappeared. Most of the vanished colonies were located close to the most populated regions of the country. The current status of the colonies in other countries is unknown. I know that several Oilbird colonies are threatened in Colombia and Bolivia.

3

THEORETICAL CONTEXT, PREDICTIONS, AND OBJECTIVES

Refuge Theory

Hamilton and Watt (1970) developed the refuge theory to explain the way animals might forage in their environment. The refuge theory was applied to animal systems that have a central place, or refuge. Some species such as honeybees, bats, and colonial birds form aggregations at central locations and from there they disperse into the surrounding habitat to forage. The hypothesis is that "the number of individuals per unit of area in the space foraged by individuals using the same dispersal center declines with distance from the core, relaxing intraspecific competition for available resources" (Hamilton, et al., 1967; Hamilton and Watt, 1970).

The refuge theory predicts that when food resources are being depleted in the vicinity of the refuge, the intake rate of an individual foraging close to the refuge eventually declines to a certain physiological threshold that negatively affects the individual. This critical situation changes the individual's foraging behavior, promoting intraspecific competition. The increase in competition reduces the net benefit for each individual up to a point where the costs of foraging are greater than the benefits. Eventually the dispersal of the individual to other places where resources are more abundant is triggered. When either the number of individuals increases at the foraging patch or the food resources decrease, the relative value of unexploited and more distant foraging patches increases.

The foraging and cave-dwelling habits of Oilbirds provide a good example of a refuge system. Oilbirds appear to have evolved novel life history traits centered on the specialization imposed by their fruit diet. Oilbirds breed and roost within their safe caves, and every night leave the refuge searching for fruit. Thus, the Oilbird offers an opportunity for studying the adaptive significance of a rare foraging strategy (frugivory) under the context of the refuge theory. I have derived a set of predictions based on both the refuge theory and the foraging habits of Oilbirds.

Predictions

Prediction 1: Tropical seasonal forests produce abundant fruit during certain months of the year. When the fruiting peak occurs, the forest can be considered an homogeneous source of fruit. The Oilbird colony inhabiting Guácharo Cave experiences seasonal variability in the availability of fruit, but because the birds forage on at least 36 species, I predict that when the colony leaves the cave in search of fruit, its foraging direction will be random during peak fruiting times. That is, the birds will head in any direction with the same probability.

Prediction 2: If Oilbirds forage according to the basic premises of the refuge theory, their home range should expand progressively through time as they follow the distribution of their food resources. Initially they should forage in the patches close to their cave, then later forage in more distant patches.

*Prediction 3:*Given the broad diet of Oilbirds, they should cover large areas, visiting several feeding places to obtain their nightly requirement of fruit. Also, since ripe fruit is produced daily, Oilbirds should visit the same food source several times until the food supply is reduced below some profitable level.

Objectives

The major goals of this study were, first, to examine the foraging ecology of Oilbirds and, second, to use the information gleaned to support conservation measures for a species threatened by expanding human activities.

For the first goal it was necessary to examine the foraging ranges, habitat use, and dispersal patterns of Oilbirds. This included determining the foraging movements, distances traveled to food sources, breadth of the diet and its annual trends, determinants of seasonal movements, distances involved, and the proportion of the population that actually moves. It was also necessary to evaluate the role of the bird as a seed dispersal agent and to examine the growth rates of nestlings in relation to the amount of food brought to the nests, food quality and availability, and brood size.

For the second goal, that of conservation, it was also necessary to determine how habitat loss influences the foraging ecology of *Steatornis caripensis* and, especially, how the destruction and disturbance of the primary forest influences the foraging movements of both the individual and the colony as a whole.

With this information now at hand it has been possible to modify the design and expansion of a new Guácharo National Park, and to provide a model for future conservation projects at other Oilbird colonies in South America.

4

METHODS

Location

The Oilbird colony studied inhabits Cueva del Guácharo close to the town of Caripe, Monagas, Venezuela. The cave is a Natural Monument existing within the Guácharo National Park, a 15,500 ha extension of seasonally dry mountainous forest in the coastal mountain range of northeastern Venezuela (Fig. 1). The area has a seasonal rainfall pattern but some rain falls most of the year. The average annual precipitation of 1178 mm is concentrated between June and November, with a peak occurring in July; it rains sporadically the rest of the year, with February the driest month. The average temperature is 21°C (meteorological station of Caripe, MARNR).

Times of Study

Field work was conducted during 1986, 1987, and 1988. In 1986 I spent six months, June to December, in the field and during 1987 and 1988, fourteen months, from June 1987 to August 1988. This field work allowed me to acquire information about the birds' foraging activities during both the breeding and nonbreeding season. Ten field assistants collaborated during the study period (see Acknowledgments). A maximum of six people worked simultaneously, but generally three to four people, including me, conducted all the activities. In terms of the time and energy needed to do radiotelemetry, the field work was costly. I estimate that 86% of the total effort and time was invested in either caving, hiking, or camping in the mountainous forest. Major problems were the large foraging area of the Oilbirds and the hilly and inaccessible topography of the region. Every time the birds changed foraging grounds, we needed three to four days to establish a new set of radio stations.

Radiotelemetry

The habits of the Oilbirds impose many restrictions on the field researcher. Traditional visual markers, such as bird bands, were useless for observations of individuals either in the field or in dark caves. Therefore, the major technique used in this study was radiotelemetry. Avian radiotelemetry is a powerful and reliable technique for monitoring bird movements and activities (Greenwood and Sargeant, 1973; Gilmer, et al., 1974; Erikstad, 1979; Herzog, 1979; Johnson and Berner, 1980; Sayre, et al., 1981). Recording the location of an unseen bird is possible using Yagi antennas which have a directional signal reception pattern that makes them ideal for this purpose (Kenward, 1987).

My portable radio equipment was obtained from Telonics (Mesa, Arizona). The basic equipment consisted of two TR2 receivers, two hand-held Yagi antennas, two 5-element Yagi antennas, two headphones, and 12 subminiature transmitters of 32 grams each. The equipment was designed to work under a variety of "Spartan" field conditions. Each transmitter weighed about 8% of the bird's weight, which is within the safe range according to Caccamise and Hedin (1985). The two-stage transmitters were designed for an operational life between eight and ten months. The equipment was tuned between 150 and 152 MHz, a commonly used frequency range for wildlife telemetry studies. Each transmitter was tuned to a different frequency within the equipment's frequency range. The TR2 portable receivers had a multiple frequency channel system that could be adjusted to the specific frequencies of the transmitters.

In determining the location of radio-tagged animals several constraints can limit the accuracy of estimations, and errors can be introduced due to topography, vegetation, weather, electrical interference, and animal movement (Hupp and Rahi, 1983). By improving line-of-sight, e.g., mounting receiving antennas on high towers or monitoring animals from aircraft, potential errors can be greatly reduced. Oilbirds forage in mountainous tropical forest that is the worst habitat for radiotelemetry studies. Tracking Oilbirds by foot or by truck turned out to be unsuccessful. Thus, I selected the highest mountains of the area as monitoring stations and these greatly increased the maximum reception distance. Nevertheless, due to the long distances flown by radio-tagged birds and the hilly topography, we periodically switched our radio stations.

We determined departure and homing directions from Guácharo Cave. After analyzing our bearings on a local map, we selected the highest mountain along that direction, which was Cerro Negro, a 2,400 m mountain, which is on average 1,000 m higher than all the mountains within a radius of 100 km. Cerro Negro is within the Guácharo National Park, about 3 km from Guácharo Cave. We set up a permanent radio station on top of the mountain, and from it determined departure and foraging directions of the tagged birds. This information allowed us to choose a potential second radio station. The second station was tested and if the tagged birds were located for most of the night, it would be selected; otherwise we would move to the next "best" potential station. Using this method we secured pairs of radio stations from which we detected signals most easily. Twelve radio stations were used during the study. To determine maximum foraging ranges we also used four temporary reception places in the lowlands along the periphery of the mountain range.

Triangulation

The position of a tagged Oilbird was ascertained by triangulation (Heezen and Tester, 1967). We tracked Oilbirds for two or three consecutive nights each week during the study period, constantly recording the position of the birds all night owing to their continuous movement. Individual birds were tracked every five minutes for up to a hour. When three or four tagged birds were detected we would switch from one to another bird every fifteen minutes. Sometimes only one or two birds remained within our reception distance all night. Even so, due to the topography, cloudiness, rainstorms, and lightning, our effective tracking time was often reduced.

Birds were located using both the "average method" and the "loudest signal method" (Springer, 1979). These techniques are possible because there are peaks in signal reception along the line of the antenna's boom, with the strongest peak to the front of the antenna. The peak gain of a Yagi is obtained with the antenna pointing directly at the signal source, and this drops about 3 dB when a three-element Yagi points about 30 degrees to either side of this line (Kenward, 1987).

There are errors associated with the triangulation of an animal's position. Besides the topographical effects, if bearings are not taken simultaneously, errors may arise due to both the bird's movement and misuse of the equipment. There are also errors inherent in the receiving system; all antennas have limited accuracy (Kenward, 1987). Adding elements to a Yagi antenna increases both its gain and accuracy. However, the higher the gain the narrower the angle or beam width in which it can be obtained. The implication is that it is easy to miss a pulsed signal if the antenna is swung around too quickly or if the animal moves too fast. For this reason I used two different antennas. The hand-held antenna allowed location of the signal quickly, whereas the 5-element antenna improved the accuracy of the bearing.

In order to decrease errors due to deflection of the signals and to the lack of synchronization in obtaining the bearings, I included two walkie talkies (Radio Shack, 3 watts) and a portable computer (Tandy 102) as part of our telemetry equipment. The walkie talkies allowed us to coordinate tracking activities from stations up to 15 km apart. When walkie talkie contact was not possible because of weather conditions or the distances involved, we always used a previously prepared schedule. In this case we synchronized our watches and followed the plan. I used a modified version of a software written in BASIC by White and Garrott (1984) that facilitated not only the estimation of a bird's position but also the storage and future analysis of the data. The program required the standard deviation of the bearings used with the maximum likelihood estimator of Lenth (1981). The program calculated the 95% confidence area of a location estimate. Next, identification numbers of the radio stations were requested. Then the bird's number (I used the radio frequency) was requested, as well as the bearings from each of the stations.

The standard deviation of our system was determined by placing a transmitter at a known location. This deviation turned out to be between 4—6°. We also set up a transmitter on top of the field truck and drove along a previously established route to determine transmitter position, bias in the readings, topographical effects, and maximum reception distance from Cerro Negro. My modified version of the program asks for the current date and time of the measurement. All the above information was stored in a file on the Tandy's random access memory (RAM). Once the values were stored, graphical and numerical outputs appeared on the display screen. The screen showed the bird's identity, its bearings, the coordinates at its location, and the area of the 95% confidence ellipse. The program facilitates *in situ* evaluation of the bird's location. When the signal was deflected and one of the stations was getting bad readings, we could correct this quickly. Radiotelemetry information was subsequently analyzed by excluding all triangulation locations that presented an angle between bearings of less than 45°. This criterion was especially important for selecting adequate remote foraging locations.

Radio-tagging

Oilbirds were captured in the Guácharo Cave using several variations of the traditional mistnetting method. Capturing adults alive within Humboldt's Gallery (Oilbirds occupy only this 800 m long initial gallery) is a challenge. Initially we set up a 12 x 2.5 m large–mesh mistnet in a section of the gallery using 6 m poles; it did not work. The birds flew so slowly that after just touching the net they would hover, back up a few meters, and turn around or fly above the net. Due to the elevation of the ceiling, we missed most of the birds. Bats were most unwelcome visitors in our mistnet. We avoided them by moving away from the bats' roosting sites and by increasing the mesh size of the net. Finally we climbed the walls of a narrow tunnel-like passage and on a ledge 15 m high we held the mistnet poles in the darkness. We successfully captured Guácharos when they left the cave at sunset and when they returned before sunrise. At these times up to 150 birds per minute flew past our mistnet. Having caught a bird, sometimes four at once, we quickly lowered the poles toward one of the team members who was ready to release the bird(s) at a lower location on the wall. The operation required four people working simultaneously. Using this nonselective method we banded and measured 500 adults and also recaptured various individuals that had been banded earlier. Differences in weights of birds entering and leaving during the breeding and nonbreeding season were recorded. We also measured and banded 100 nestlings.

For each captured bird we measured wing length, wing span, second primary feather length, wing width, body length, tarsus length, gape width, beak length, and weight. The species is not sexually dimorphic, so sex could not be determined visually. We laparotomized several Oilbirds and learned that males are slightly larger and stronger than females (Table 1).

Ten Oilbirds were kept in captivity for two days to watch their behavior after radio-tagging, using a cotton-nylon harness to hold the transmitter on their backs. Young fledglings and relatively weak and light individuals were unable to fly properly, but strong birds weighing between 370-410 grams carried the transmitters without apparent problem. We determined the relative strength of the birds subjectively as they were handled. Mistnetted Oilbirds were selected subject to the above criteria and were released immediately after radio-tagging. Using this method 11 adults were radio-tagged during the study period. We never released more than one bird at a time.

The above procedure had nonselective aspects. There was no way to determine the bird's breeding status, nesting place, or the accessibility of its nesting or roosting site in the cave. The latter was important in order to obtain information about the bird's breeding status and how this related to its foraging trips. The most difficult thing we tried was to radio-tag specific birds nesting in solitary nests. Using a red filter on our headlights we quietly climbed the walls to a point directly above or underneath the nest. We stayed there with our lights off for about an hour and then, with a hand-held net, tried to capture the bird as fast as possible. During the breeding season Oilbirds are extremely sensitive to human intrusion around their nesting ledges and immediately abandon their nests when disturbed.

We sedated adult Oilbirds once they were caught, having first experimented with domestic chickens to determine the effects and dosage of the anesthetic in relation to the animal's weight. The anesthetic was administered intravenously through the subclavian vein using insulin syringes. In 30 seconds a dosage of 1 ml/bird of cifarcaine sedated the bird. The recovery time was about 40 minutes. Sedated birds were put back on their nests and observed. If we followed the proper procedure quickly, the birds would not abandon the nest. Using this method we captured a nesting pair just after their nestlings had hatched. Only the male was radio-tagged (No. 065). The pair not only went out to forage the same night, but also remained at the nest (Nest No. 10) for the remainder of the breeding season.

5

OBSERVATIONS

Radiotelemetry Data

Table 1 shows basic information about the radio-tagged Oilbirds during the study period 1986-1988. Eleven Oilbirds, five females and six males, were tagged. These birds were tagged in groups of four, three, and four individuals. Because Oilbirds are monomorphic, and because I did not attempt laparotomy on the first four birds, errors in sexing birds are possible.

The radiotelemetry data obtained cover the seasonal movements of the birds through their reproductive cycle. Radiotelemetry nights ranged from a minimum of one to a maximum of 23. This variation was due to the remoteness of the areas where the Oilbirds foraged. Not all the birds presented the same probability of being monitored from a given pair of radio stations. Some individuals (e.g., Nos. 255, 045, and 066) were hard to track after they were released. Others (e.g., Nos. 175, 195, 214, and 065) were tracked more intensively for extended periods of up to seven months.

Basic Foraging Pattern

My radiotelemetry data are not evenly representative of all tagged birds (Table 1). Some individuals are represented by many bearings, others by few. This could bias the resulting distribution of the frequency of bearings. Additionally, the set of triangulation locations obtained any given night from a tagged bird raises questions about the degree of independence between the various data points of that bird. It is feasible that Oilbirds may make foraging decisions based on both previous experiences, and interactions with other individuals. If this happens, the foraging locations are not independent events. To satisfy statistical requirements and to avoid the independence problem, there was determined, in the case of the rank-sum test, a mean vector per night and per study period for each tagged bird. Additionally, the statistical analyses presented in this section include radiotelemetry data restricted mainly to departing foraging directions. When possible I excluded close foraging locations and the movements of birds within a small foraging area for a given night. These criteria increased the degree of independence among the observations and at the same time gave sufficient data points per bird to do the analysis.

Table 1. Summary of radio-tracking information.

Year	No. Tracked	Bird No.	Tracking nights/bird	Av. tracking nights	Hours Telemetry
1986	4	115	22	18.00	220
		134	19		190
		275	13		130
		235	18		180
1987	3	175	23	11.23	230
		195	7		70
		214	4		40
1988	7	214	1	4.282	10
		065	18		180
		255	2		20
		045	3		30
		066	1		10
		175	1		10
		195	4		40
				Total	1,360

Bird No.	Release Date	Months Tracked	Weight (gr)	Sex	Comment
115	23 Sept. '86	Sept.-Dec. '86	360	M(?)	Non-breeding season
134	23 Sept. '86	Sept.-Dec. '86	350	F(?)	
275	23 Sept. '86	Sept.-Dec. '86	370	M(?)	
235	07 Oct. ' 86	Oct.-Dec. '86	350	F(?)	
175	16 July '87	Jul.-Oct., Dec. '87-Jan. '88	400	M	End of breeding season plus breeding season
195	13 Oct. '87	Oct.-Dec. '87-Jan., Apr.-June '88	410	M	
214	27 Oct. '87	Oct.-Dec. '87-Jan. '88	390	M	
065	16 Apr. '88	Apr.-July '88	405	M	End of non-breeding season plus all breeding season
255	06 Apr. '88	Apr.-June '88	395	F	
045	21 Apr.'88	Apr.-June '88		F	
066	27 July '88	July '88	300	F	

The radiotelemetry data are shown following basic techniques of circular statistics (Batschelet, 1981). Oilbirds exhibited a multimodal distribution resulting from various overlapping unimodal distributions. In circular statistics the multimodal and unimodal distributions are analyzed differently. In general, the unimodal distributions are analyzed using the Rayleigh test (Batschelet, 1981). This test requires a random sample of angular values representing directions in a plane and determines whether the population from which the sample was obtained differs from random. It tells us whether the sample has any directionality. Axial distributions still can be converted into unimodal distributions without changing the method of analysis. Multimodal distributions require different tests such as the chi-square test (Batschelet, 1981). The Rayleigh test assumes that the **r** statistic has been estimated using the formula:

$$r = (x^2 + y^2)^{1/2}$$

$$\text{where } x = 1/n\ (\cos\phi_1 + \cos\phi_2 + ... + \cos\phi_n)$$

$$y = 1/n\ (\sin\phi_1 + \sin\phi_2 + ... + \sin\phi_n)$$

$$n = \text{number of observations}$$

The mean angle of the sample is defined as,

$$z = \arctan(y/x), \text{ if } x > 0$$

$$z = 180 + \arctan(y/x), \text{ if } x < 0$$

The null hypothesis **Ho**, is "The parent population is randomly distributed." **Ho** was tested by comparing **r** with critical values in Table H of Batschelet (1981).

The chi-square test can be used to test for randomness. To apply the chi-square test, the circle is subdivided into a number of arcs. The number of data points in each arc is determined and the expected frequency from the given circular distribution is obtained. The null hypothesis **Ho**, "the parent population coincides with the given circular distribution," is tested using the chi-square statistics as in linear statistics. In this test, **k** is the number of groups, $\mathbf{n}_i$ are the observed values, and $\mathbf{e}_i$ are the expected values ($\mathbf{e}_i = \mathbf{n}/\mathbf{k}$), where **n** is the sample size. The test has $\mathbf{v} = \mathbf{k}\text{-}\mathbf{1}$ degrees of freedom.

Using a rank sum-test (Batschelet, 1981) it was determined whether the mean angles of the distribution of the bearings of tagged birds and the frequency distribution of the primary forest differed significantly from each other. The test is a modified version of the Wilcoxon-Mann-Whitney test. The basic idea of the rank-sum test is to pool the mean vectors of both samples and rank the **n** + **m** observations. In this case **n** represents the mean vectors **ßn**'s of sample No. 1 and **m** represents the mean vectors **øm**'s of sample No. 2. The test assumes that **m** £ **n**. To make the test statistic independent of the arbitrary zero direction the **N** = **n+m** observations must be ranked in such a way that the sum of ranks of the **ßn**'s (smaller sample size) turns out to be a minimum. The test statistic is defined as:

$$U = S - 1/2m(m+1)$$

where S = the minimum rank sum

A total of ten (**n**=10) mean vectors, one per tagged bird, were determined and analyzed with seven mean vectors (**m**=7) obtained from the estimated distribution of the primary forest. The mean vectors of the forest were calculated by pooling the frequency values in approximately 51° arcs.

Forest Quantification

From the top of Cerro Negro, as well as from other stations, we had a panoramic view of the entire mountain range. By using a local map the general distribution of the primary forest was determined. Because I could not measure the extensive mountainous forest of the region, I assigned arbitrary values from one to five to the vegetation in a given area. A value of one equaled a low proportion of primary forest, with mostly secondary forest, coffee plantations, towns, and in some cases, slashed-and-burned areas. A value of five equaled a very high proportion of primary forest. Using this method, I obtained an indirect estimation of the amount of primary forest for each ten degree arc around the top of Cerro Negro.

The Caripe mountain range may be considered as an enormous island. The northern topography changes abruptly from sea level to 2,400 m at the top of Cerro Negro. From Caripe it takes only 45 minutes driving to reach the Gulfs of Cariaco and Paria. The vegetation associated with this elevational gradient changes accordingly. From a mature primary forest in the Caripe area the vegetation changes to a more bushy and xerophytic vegetation to the north. The southern topography changes in a more gradual way, but again the lowland habitat is very different from the forest of the higher elevations. The lowlands are savanna habitat that has been heavily altered by humans. The savanna is an enormous grass-covered plateau with scattered palm trees and bushes, intertwined with rivers. The region contains most of the agriculture and cattle ranching areas within the state of Monagas.

6

ANALYSIS

Departure Directions

The population showed significant evidence of nonrandomness in the direction in which it departs the cave. Although Oilbirds left in many directions during the breeding season, observations fell mainly between 0-180°, **r**=0.70, **d**=92°.31 (Figs. 2, 3; Table 2). The result apparently does not support the proposed hypothesis derived from the refuge theory. The null hypothesis, that the population has a random distribution, has to be rejected.

The refuge theory assumes that resources are evenly distributed, but during three years of observation I found that those around Guácharo Cave were not uniformly scattered (Fig. 4). The distribution is skewed toward the east (**r**=0.39, **d**=133°.24) because the west mountain forest of the "Cerro Turimiquire" region is one of the most disturbed areas of northeastern Venezuela (Huber and Frame, 1989). Major factors that influence the primary forest distribution are the east–west orientation of the Caripe mountain range, and the presence of coffee plantations and orange groves. The local landscape is a mosaic of patches of

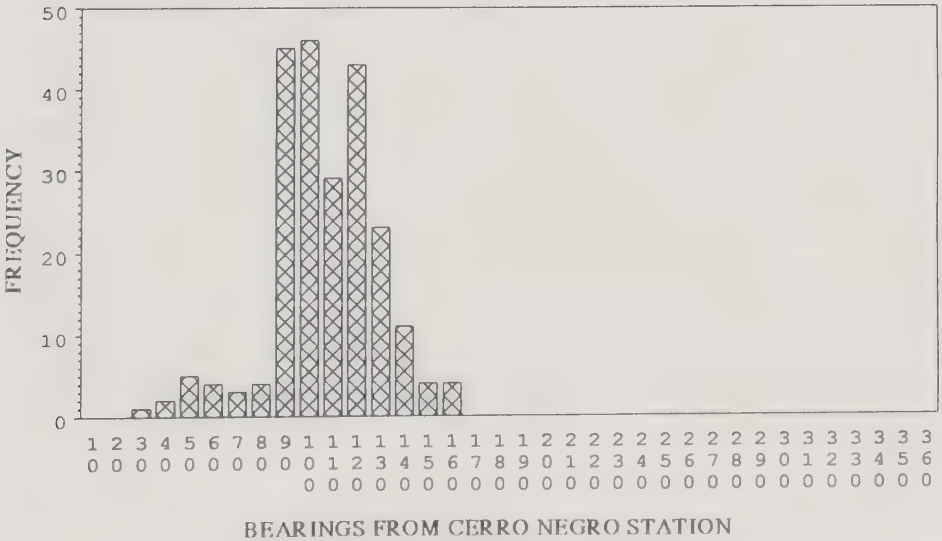


Fig. 2. Departure directions for 10 tagged birds between April and August 1987-1988. The bearings are grouped in ten degree arcs. The data were collected from Cerro Negro during the first two hours after the birds left Guácharo Cave.

Table 2. Circular statistics parameters (mean angles and standard deviations) of ten tagged birds and of the distribution of primary forest.

Bird No.	N	r	Mean Angle (degrees)	S (radians)	S (degrees)
066	6	0.99	49.06	0.1273	7.29
175	65	0.62	75.42	0.8671	49.68
195	9	0.98	94.56	0.1807	10.35
214	9	0.99	103.52	0.1169	6.70
115	10	0.98	110.60	0.1580	9.05
134	9	0.92	113.60	0.3960	22.69
065	25	0.57	137.83	0.9195	52.68
235	10	0.99	139.85	0.0925	5.30
255	5	0.98	223.34	0.0658	3.77
045	5	0.99	256.09	0.0647	3.70
All Birds	153	0.70	92.31	0.7617	43.64
Forest					
*0—50°	8	0.97	36.29	0.2495	14.01
50—100°	18	0.96	82.70	0.2511	14.38
100—150°	22	0.97	127.77	0.2339	13.40
150—200°	18	0.88	197.47	0.4831	27.68
200—250°	7	0.97	228.47	0.2164	12.40
250—300°	5	0.97	267.90	0.2020	11.62
300—350°	9	0.95	344.45	0.3161	18.11
Total	78	0.39	133.24	1.1009	63.07

* For simplicity in notation the forest data are divided into seven groups using whole numbers. Notice that the last group ranges from 300 to 350. It should be 301.42 to 360 because each arc is 51.42 degrees instead of 50. The same comment is valid for remaining groups. This change, however, does not modify the calculations.

primary and secondary forest around larger towns, with primary forest in more distant places. My habitat analysis assumes that the distribution of the food corresponds with the distribution of the mountainous forest. Thus redefined, my initial hypothesis becomes: "The distribution of the departure directions of foraging Oilbirds should not be different from the distribution of the primary forest around Guácharo Cave."

I tested this hypothesis using a rank-sum test (Batschelet, 1981). For **n**=10, **m**=7, **S**=47, and **U**=19, Table U (see Batschelet, 1981) yields **P** > 0.100. With $\alpha = 0.05$, I concluded that the two samples are not significantly different. Thus, the redefined null hypothesis cannot be ruled out.

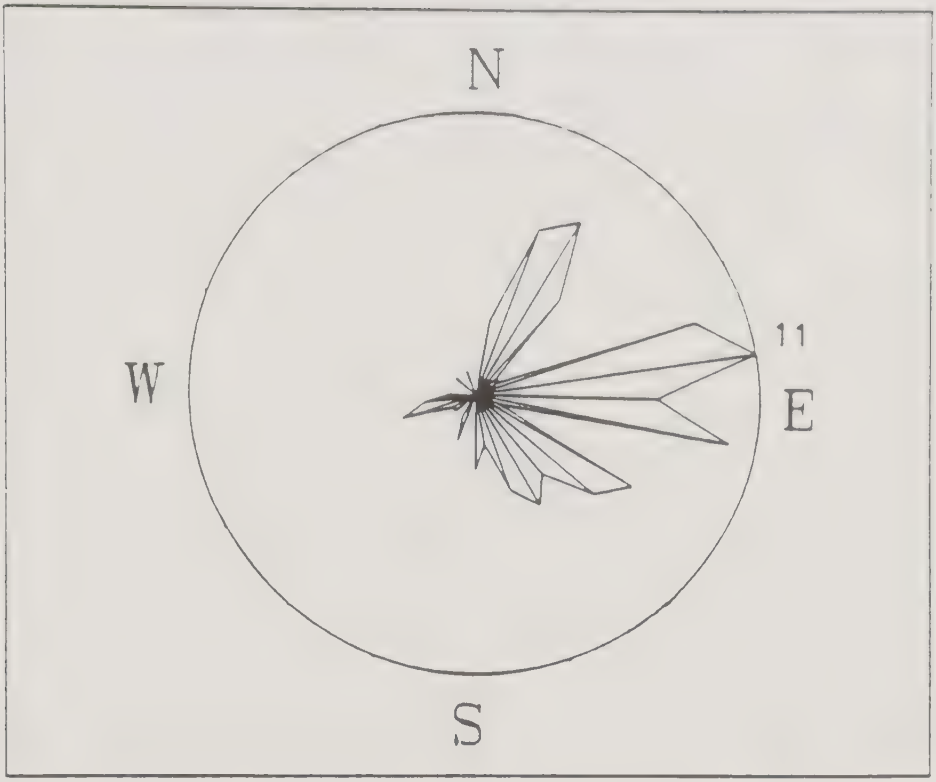


Fig. 3. Grouped data showing departure directions and frequencies for 10 tagged foraging birds between April and August 1987-1988. The length of each line within the circle indicates absolute frequency of bearings. The highest frequency is represented by the radius (11 in the figure). The bearings are pooled in ten degree arcs.

In a mosaic habitat, Oilbirds avoided disturbed forests, but in primary forest the foraging movements of the colony were random. Not all birds went in one particular direction at a time. Usually a large group of several hundred departed in one direction and other groups departed in different directions. The birds procured their fruits mostly where the suitability of their food plants was the highest. Less suitable habitats, such as secondard forest, were less often visited. Several questions arise concerning foraging patterns: Did oilbirds change frequently from one feeding area to another? Or did they stay in one area, revisiting the same places every night?

Individual Foraging Directions

Radiotracking showed that the foraging movements of individual Oilbirds are nonrandom. The direction toward which each departs reflects a preference for a

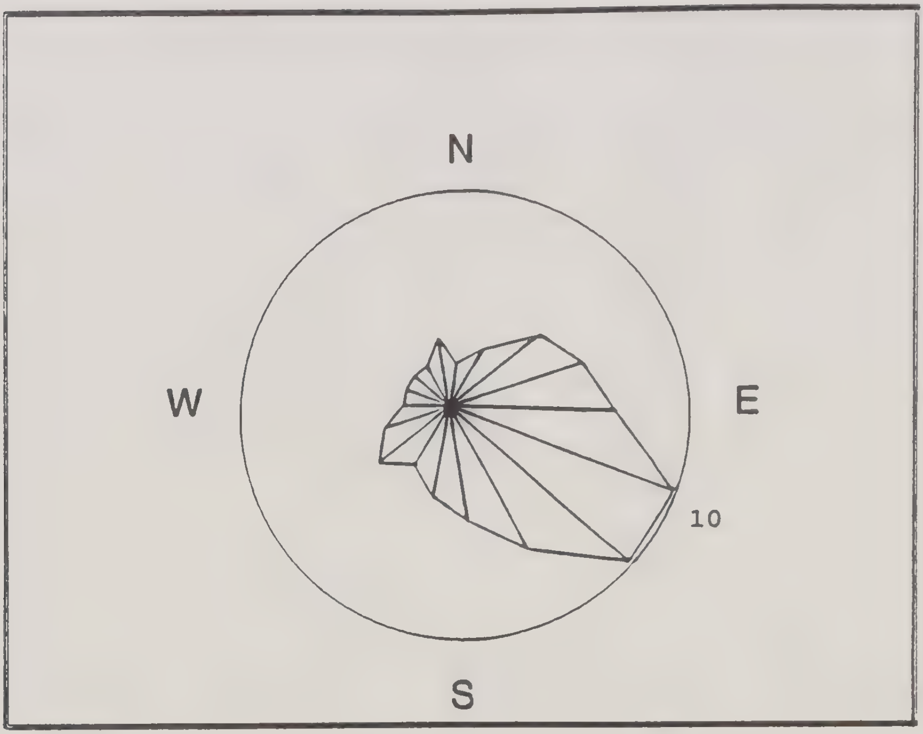


Fig. 4. Distribution of the proportion of primary forest in the study area. The figure was generated using the summit of Cerro Negro as the central point. Forest distribution was estimated within a range of 60 km. Within each ten-degree arc an arbitrary value between 1 and 5 was used to indicate forest proportion; e.g., 5 indicates undisturbed primary forest. The values are grouped here in twenty degree arcs. The highest frequency is represented by the radius (10 in the figure).

specific foraging area. Every individual consistently goes to the same general foraging place whether it is breeding or not. It appears that the cumulative effect of numerous individuals foraging in different areas yields the random foraging pattern found at the colony level.

The colony as a whole foraged in all directions, depending on the distribution of the primary forest. Individuals, however, showed different foraging patterns. Figure 5 shows the foraging directions taken by three tagged birds. The null hypothesis **Ho**, tested on these birds (Nos. 175, 065, and 195), assumed that the birds took a random direction each time they departed to forage. In all the cases **Ho** was rejected (Table 3). Bird No. 175 showed a bimodal distribution with two distinct foraging directions. It concentrated its movements toward the northeast and east between 20° and 100° and was never tracked between 40-60°. The bird also occasionally went toward the south. Its movements were not random ($X^2 = 95.8$; $P < 0.001$). The bird showed a strong preference to forage toward the 30°

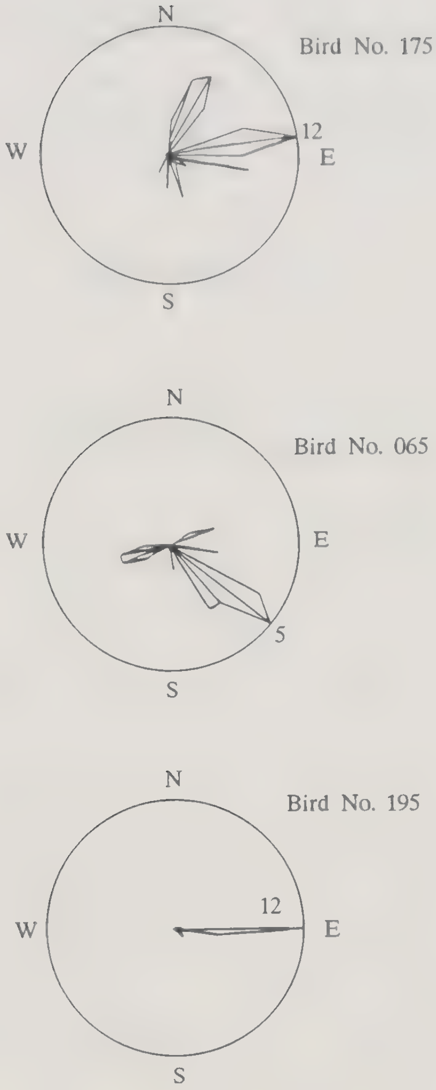


Fig. 5. Grouped data indicating departure directions and frequencies for foraging birds Nos. 175, 065, and 195 between April and August 1987-1988. The length of each line in the circle indicates the absolute frequency of bearings. The highest frequency is represented by the radius (e.g., 12 in the figure for bird No. 175). The bearings are pooled in ten degree arcs.

and 80°. The bimodal distribution of the bearings of No. 175 correspond with the two foraging areas the bird exploited during the season.

Bird No. 065 also showed a mostly bimodal distribution of its foraging trips. Most flights were taken between 120-260° with a few trips toward 60°. The foraging movements of No. 065 were not random ($X^2 = 61.7$; $P < 0.001$). This bird presented a very predictable behavior. Every night it left the cave about 19:00 h

Table 3. Chi-square test of foraging directions of tagged birds.

Source	**Chi-sq.**	**N**	**V**	α	**P***	**Comment**
Angles from all birds	76.89	112	17	0.05	<0.001	Reject Ho
Angles from brid no. 175	95.79	75	17	0.05	<0.001	Reject Ho
Angles from bird no. 065	61.66	27	17	0.05	<0.001	Reject Ho

Rayleigh Test				
Source	r value	N	P*	
Angles from bird no. 195	0.8576	23	<0.001	Reject Ho

* Critical value from Table G (Batschelet 1981). All bearings taken from Cerro Negro.

and flew straight to its foraging grounds. Bird No. 065 foraged constantly in the same general area and the bimodality of its bearings reflects the way the bird exploited its feeding localities. It foraged on two major patches of forest. Its foraging directions did not overlap with the directions of Bird No. 175. No. 175 foraged toward the northeast and No. 065 foraged toward the southeast and southwest of Guácharo Cave. Because we obtained information about No. 065's movements from various stations other than Cerro Negro, the frequencies of bearings of Figure 5 represent only a partial set of data points. Bird No. 065 foraged mainly toward the southwest.

The foraging movements of Bird No. 195 showed extreme directionality. It showed a very strong preference for the 90° direction. It was captured and released in October 1987, at the end of the breeding season. It abandoned Guácharo Cave and went to another cavern system in the region where it roosted in a new cave and changed foraging grounds. Its signal was lost. After two months, in January 1988, it returned to Guácharo Cave but did not stay long. Once more we lost it for several weeks, but at the beginning of the breeding season we found its signal again in Guácharo Cave. Soon we realized that this male was not breeding and it was "commuting" from Guácharo Cave to other caves in the southeast. Possibly when we obtained its weak signal it was foraging exceptionally far away from our Cerro Negro station.

From No. 195 we learned that some members of the colony that are not paired may become floaters and move from one cave to another. Perhaps they eventually find a mate and an adequate nesting place. It appears that during the breeding season while most of the colony members are feeding their offspring and constantly returning to the nesting cave, some unpaired Oilbirds are moving to other areas where they may interact with birds of other colonies.

Foraging Areas

Different statistical methods have been used to study spatial patterns of living populations in their natural environment (Pielou, 1977). The way the foraging positions of the birds were sampled through radiotelemetry generated a spatial pattern that raises questions, such as, what will the observed frequency distribution be like and how can it be explained? Figure 6 suggests that there is a certain degree of aggregation in the feeding areas. The variance to mean ratio, **V/m**, is a generalized and simple way to measure aggregation. The method is based on the defining property of clumped discrete distributions in which the variance exceeds the mean for all of the cases (Pielou, 1977).

$$\text{Variance} = (1/nX) \quad _{j1} (X_j - X)^2$$

> Where $\mathbf{X}_j$ is the number of observations in the $\mathbf{j}_{th}$ of **n** units sampled, and $\mathbf{X} = (\ \mathbf{X} \ _j/\mathbf{n})$. For a large **n** the expected value of the ratio **E**(**V/m**) is approximately 1 when the individuals are dispersed at random (Sokal and Rohlf, 1981).

I arbitrarily divided the study area as plotted in Figure 6 into 252 grid cells. Each cell was 1,732 m wide giving an area of 3 km^2 per cell. The criterion for choosing that area was a function of both the distances between consecutive feeding places, in general between 100 and 500 m, and of the restrictions associated with the triangulation of tagged birds from two stations. The grid covered an area 63 km x 39 km (2457 km^2). I counted the frequency of observations and then obtained the variance to mean ratio (**V/m**).

Figure 6 shows the foraging places visited by 10 tagged Oilbirds during the breeding season. Each circle represents a single visit. The data were gathered from 12 radio stations scattered through the home range of the Oilbirds. The blank areas are places never visited by the tagged birds. Those areas, like blank areas among the more clumped points, are heavily disturbed habitats where towns, coffee plantations, and orange groves occur. Coffee plantations are less deleterious to the Oilbirds than other kinds of disturbed habitat because when clearing the forest, some tall trees are left to shade the coffee shrubs. Some of those trees are members of the Lauraceae and Burseraceae and are food plants for Oilbirds.

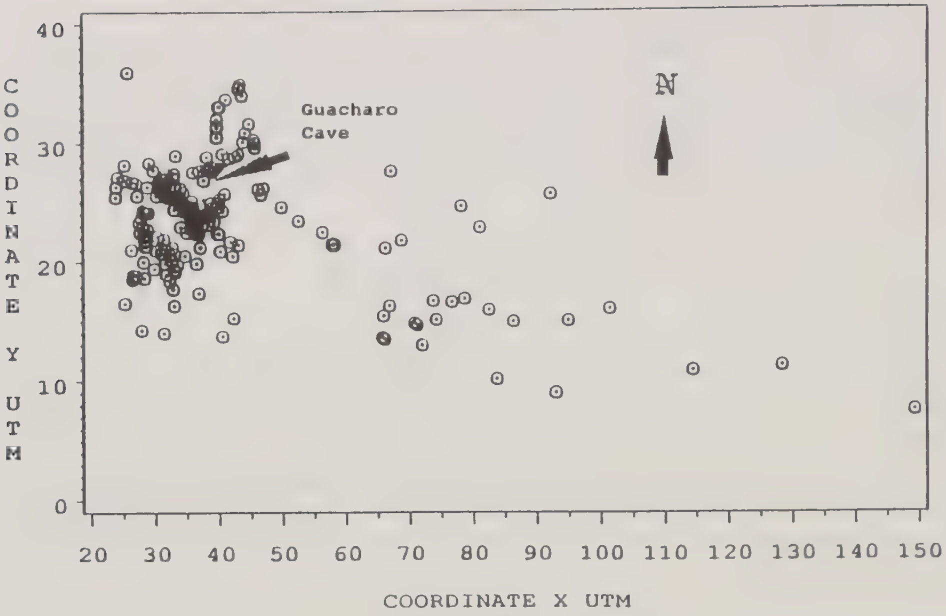


Fig. 6. Foraging areas of 10 tagged birds from data collected between 1986-1988. Each of the 240 circles represents a location obtained by triangulation. The coordinates correspond with the Universal Transversal Mercator System (UTM). To simplify numbers, the last two digits of the Mercator grid are included. 1 UTM unit = 1 km.

Oilbirds show exceptionally long foraging movements. On any night Oilbirds may travel as far as 100 km from Guácharo Cave, although most of their foraging occurs in a 40 km radius from the cave. The variance to mean ratio (**V/m** = 10.96/ 0.841 = 13.02) clearly shows that the feeding areas of the Oilbirds present a "contagious" arrangement. Though most of the localities were counted (218), I did not include in the analysis the most distant data points. If they had been included, the variance in relation to the mean would have been still higher, yielding an even higher ratio. The aggregations of feeding areas of these birds are conspicuous and the foraging patterns correspond to the clumped distribution of the feeding grounds. The aggregation might be the result of both habitat destruction and preference for particular patches of primary forest. Although the birds foraged mainly within a radius of 40 km around Guácharo Cave, the potential for more distant foraging is striking. The rest of the foraging localities were scattered, mainly southeast of the cave. The maximum distance between feeding localities is about 150 km.

Foraging Areas and Home Ranges

Using the radiotelemetry data, the "contagious" nature of the feeding localities was examined. The nature of the radiotelemetry information and the way the mountainous primary forest is distributed hinder defining discrete foraging patches. Some forested regions are enormous and the birds go to specific locations within these areas. Some birds switch to another location the same night. I have used the movements of the birds themselves to define what could be a foraging patch.

Oilbird No. 175 was tracked for four months during the nonbreeding season of 1987. Bird No. 065 was also monitored for the same amount of time but during the breeding season of 1988. The nocturnal trajectories of the birds during the study period were plotted as a solid line and the feeding areas were joined with the solid line following a chronological sequence (e.g., Fig. 7). In this way the figure of the foraging movements of the birds corresponds with the exact way they used their habitat through time.

The chronological sequence of the coordinates of different birds provides a useful way to understand how the birds exploited their foraging patches. For a time-sequence analysis of both Oilbirds, the X coordinate was chosen because the tagged birds' foraging distances in relation to the cave are better illustrated.

Radiotelemetry locations were used to determine home ranges for Birds Nos.

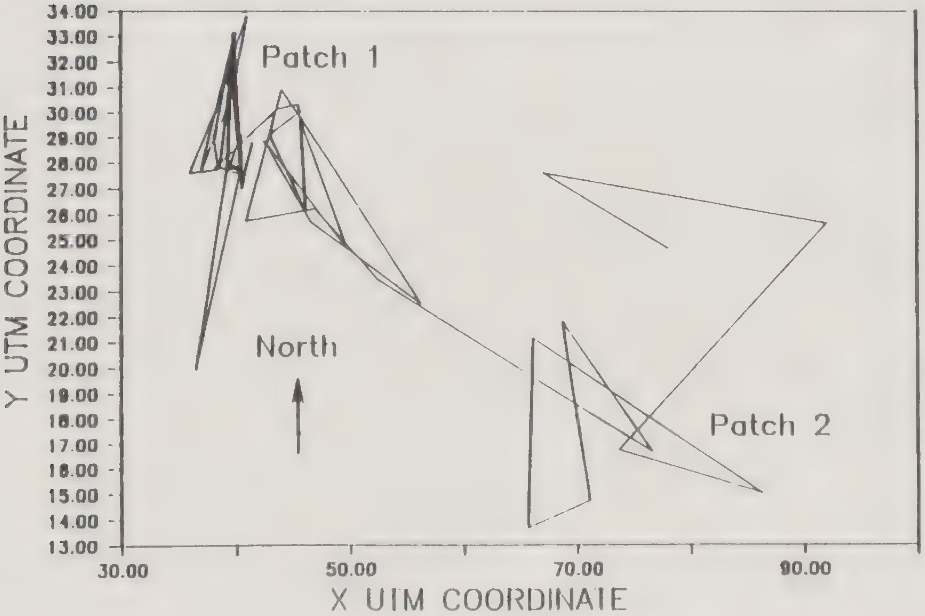


Fig. 7. Foraging patches of bird No. 175. Patches 1 and 2 were defined by plotting the nocturnal movements of the bird following a chronological sequence, July-October 1987.

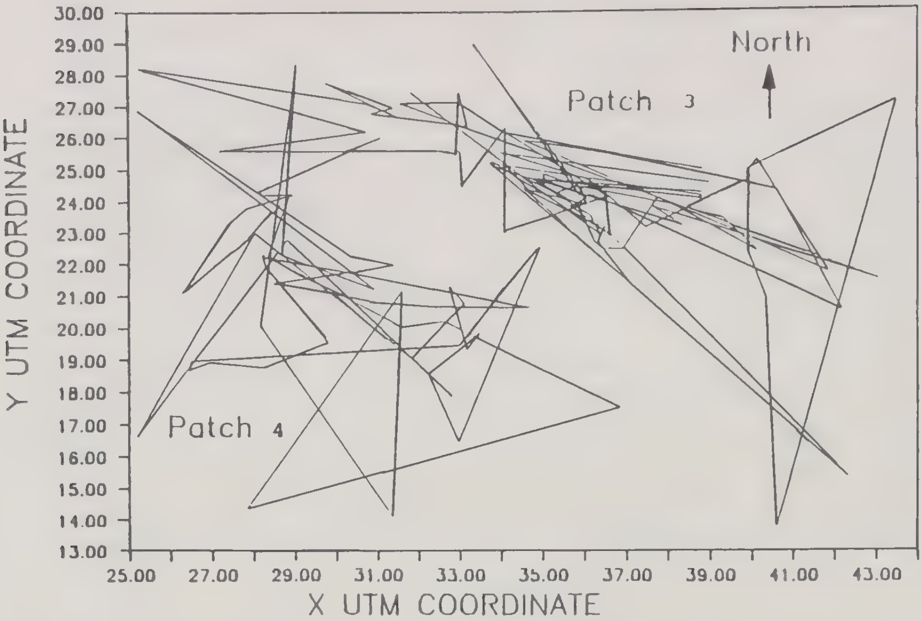


Fig. 8. Foraging patches of bird No. 065. Patches 3 and 4 were defined by plotting the nocturnal movements of the bird following a chronological sequence, April-July 1988.

175 and 065 (Figs. 7, 8). The contour lines, or isopleths, were obtained through the harmonic mean transformation method of Dixon and Chapman (1980). Contour lines from 20 to 95% of the observations are shown. A contour line including 100% of the data points was not included in the analysis because it would have yielded extremely large values for the home range. This happens when additional data points occur away from most of the points and show very low frequencies.

Figures 7 and 8 show how two Oilbirds, Nos. 175 and 065, foraged in the mountainous forest. The data presented are the most detailed and extensive from all the birds tracked and show that individuals exploit discrete patches of primary forest. The nocturnal movements of each bird were restricted to two major foraging areas. The areas used by each bird differed in size, intensity of use, location in relation to the cave, and distance between them. Within a patch Oilbirds might visit the same feeding places several times.

In their use of particular foraging patches Oilbirds were consistent from night to night. Patch use seems to be strongly influenced by the mosaic distribution of suitable foraging resources in the study region. Perhaps a significant reduction in available fruit around Guácharo Cave forces the birds to go to better and more remote regions.

The foraging areas of Bird No. 175 were north and east southeast of the cave

(Fig. 7). Patch 1, mainly 80° north from Guácharo Cave, is only 8 km away from the cave. Patch 1 encompasses a mountainous zone characterized by deep canyons and waterfalls. It is outside the boundaries of the Guácharo National Park. Bird No. 175 foraged in Patch 1 in July and August. At the end of August the bird changed its foraging movements and shifted toward the east, exploiting the periphery of Patch 1. At the beginning of September it moved to a different area, Patch 2, and did not return to Patch 1. Patch 2 is 25 km southeast of the cave. The bird foraged in Patch 2 during September and October. At the end of October it abandoned Patch 2 and did not return to its foraging grounds, dispersing to another area (see p. 41).

Oilbird No. 065 showed a more complex foraging pattern than No. 175 (Fig. 8). It is apparent that this bird also foraged in two major patches although they are slightly less differentiated than in the case of Bird No. 175. Patch 3 included Guácharo Cave and was within the park's limits. Number 065 foraged first in a radius of 6-8 km around the cave but more often to the west. The density of the solid lines in Figure 8 is greater in Patch 3 than in Patch 4, indicating that No. 065 used Patch 3 more intensively. No. 065 visited the same feeding places in the western sector of the patch several times. It is quite possible that the bird was exploiting the same fruiting trees within the patch. Patch 3 is a hilly forested area where the limestone rocks have been heavily eroded. In this area there are several waterfalls and secondary rivers where aromatic laurels are common. No. 065 foraged in Patch 3 from April to mid-May. At the end of May the bird started to move toward a new area, in Patch 4, but it did not abruptly abandon Patch 3. Every night it left the cave following the same general route. It was consistent in terms of its departing time, always about 1900 h, and in its preference for certain foraging patches. It would go through Patch 3 first, and then switch to Patch 4. Patch 4 is on average 10 km away from the cave and outside the park's border. No. 065 foraged this patch, gradually increasing the distances until it reached the farthest sections, 15 km away from the cave. Bird No. 065 foraged in this patch until the end of July, when it moved to another area. The number of trips Bird No. 065 took to feed its offspring decreased from three per night the first month (April), to one per night at the end of the breeding season (August).

The birds foraged first in the patches closest to the cave for 6 to 8 weeks and then switched to more distant areas. The distance between patches changed markedly. During the first two months the X coordinates of No. 175 varied little (Fig. 9). The observed pattern probably means that once the bird arrived at Patch 1 it would forage mainly along a north-south direction. The bird followed this general direction back and forth, probably visiting the same fruiting trees several times. This pattern is more apparent in the northwest section of Patch 1. During the last two months, however, No. 175's coordinates changed abruptly, reflecting its switch to another patch. The foraging behavior of No. 175 at this time was less predictable. The bird changed more frequently from one feeding place to another

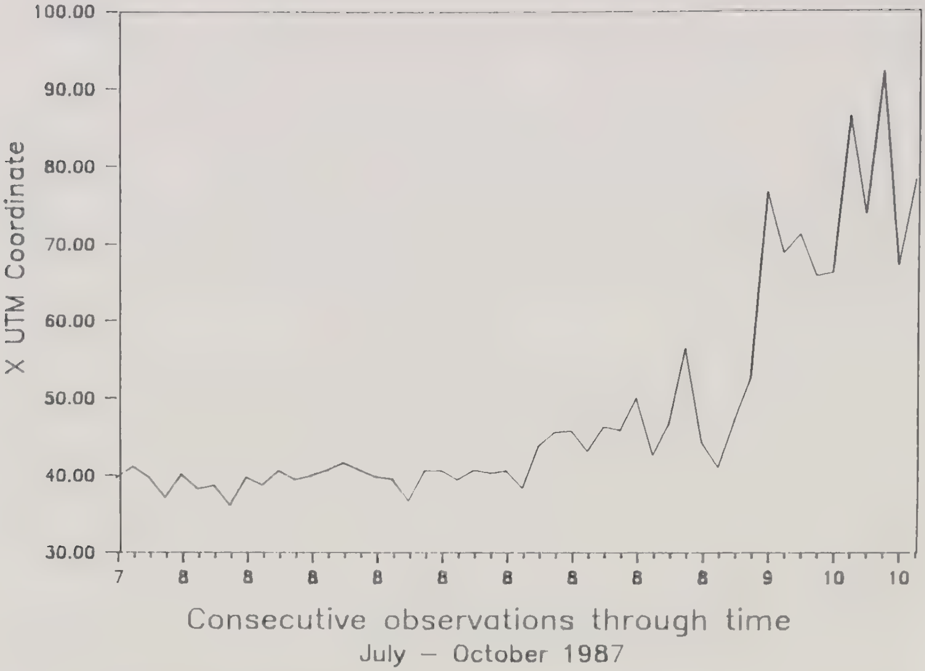


Fig. 9. Time-sequence analysis of the X UTM coordinate of bird No. 175. The coordinates were sorted as consecutive observations between July and October 1987. The numbers along the X axis indicate the month of the observation. The Y axis indicates how the X UTM coordinate changed over time.

within Patch 2. Nevertheless, the bird used Patch 2 with less intensity than Patch 1.

The most striking feature of Figure 9 is that the values of the X coordinate grew at an increasing rate starting at the end of August. Bird No. 175 had to fly farther each time to find a suitable new foraging spot. The general area where the bird foraged encompassed the towns of Sabana de Piedra, Tierra Blanca, and La Guanota, a road that leads to the town of Santa Maria, and an area to the east known as Mata de Mango. Aside from the secondary forest and coffee plantations typical of this zone, there are several barren slashed-and-burned mountains. This might explain the long-range foraging movements of No. 175.

Bird No. 065 showed a very different pattern regarding the amount of change in its X coordinate (Fig. 10). For almost two months No. 065 foraged mainly in an east-west direction. Most fluctuations in the value of the X coordinate in this period varied from the mid-30s to the 40s. The changes in the X values to 40.00 corresponded with movements of the bird back to the cave; its return trips were also much more frequent than those of Bird No. 175. This was because No. 065 was breeding. Oilbird No. 065, a male, when tagged and released in April 1988,

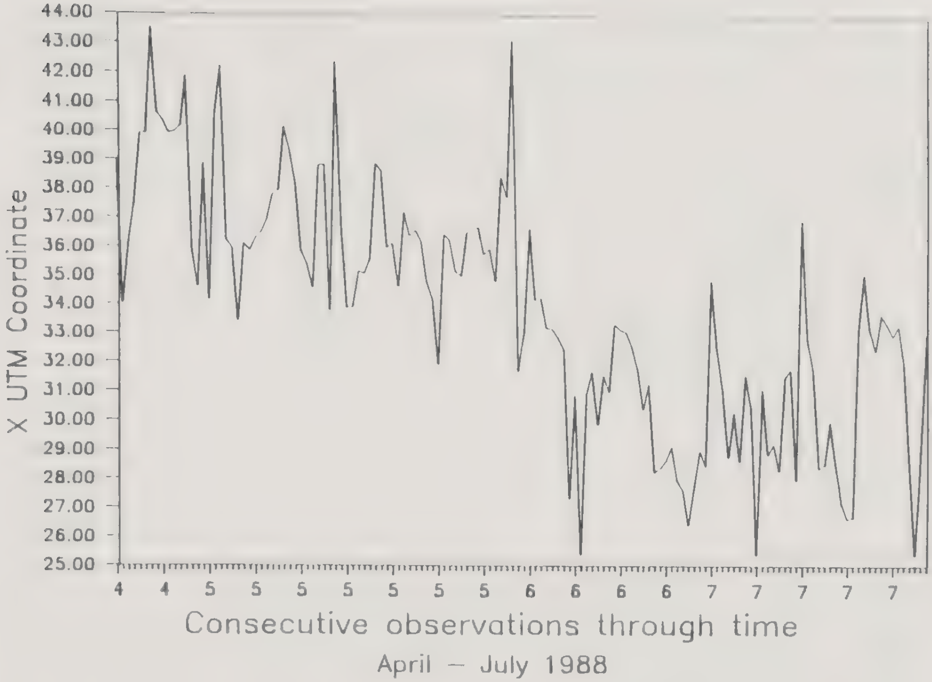
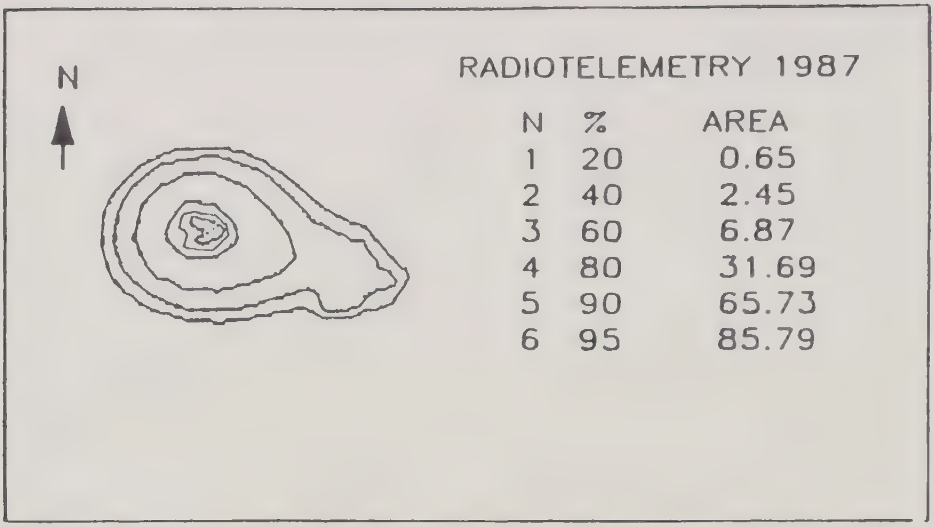


Fig. 10. Time-sequence analysis of the X UTM coordinate of bird No. 065. The coordinates were sorted as consecutive observations between April-July 1988. The numbers along the X axis indicate the month of the observation. The Y axis indicates how the X UTM coordinate changed over time.

had three newly hatched nestlings. The foraging movements of this breeding bird were dedicated to collecting enough fruit for its offspring. On the other hand, No. 175 was not breeding; perhaps its foraging movements were mainly devoted to fulfilling only its own metabolic requirements.

At the beginning of June, No. 065 also showed an abrupt switch in its coordinates from values of 32-25. These values corresponded to its new foraging patch. The important feature of the curve in Figure 10 is that it also shows a rather abrupt change when the average values are considered and when the return trips are excluded. This area along the southwest border of Guácharo Park contains the towns of Periquito, El Palmar, El Rincon, and several smaller villages where there is much habitat destruction. Bird No. 065 avoided these areas in finding adequate foraging grounds.

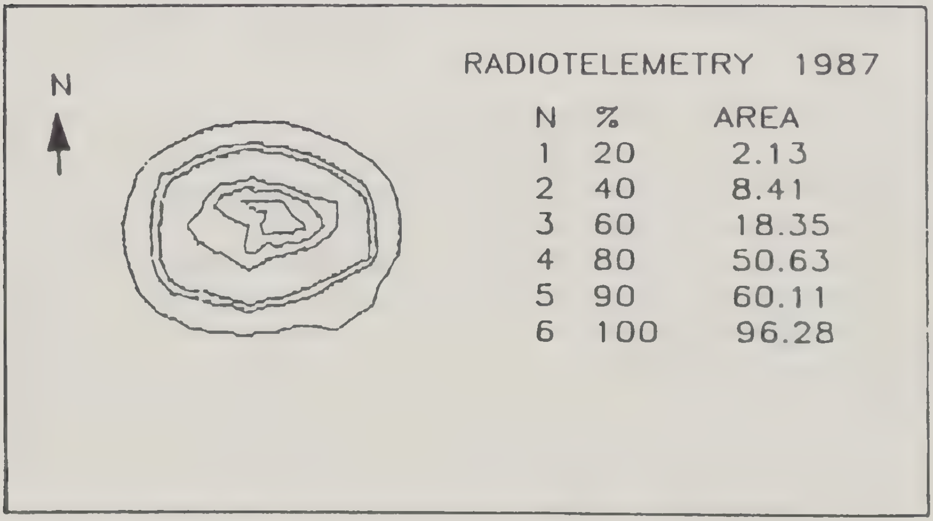
Both birds showed home ranges of about the same size. The best estimation of the home range value for No. 175 is 85.79 km^2. That value corresponds with the last isopleth (Fig. 11). The figure also indicates the center of activity within the bird's home range. This center is displaced toward Patch 1. This corroborates that Patch 1 was used more intensively than Patch 2. Figure 12 shows the estimated



RADIOTELEMETRY 1987

N	%	AREA
1	20	0.65
2	40	2.45
3	60	6.87
4	80	31.69
5	90	65.73
6	95	85.79

Fig. 11. Home range of bird No. 175. The contour lines contain up to 95% of the foraging areas of the bird. The isopleths were estimated using the harmonic mean transformation method of Dixon and Chapman (1980).



RADIOTELEMETRY 1987

N	%	AREA
1	20	2.13
2	40	8.41
3	60	18.35
4	80	50.63
5	90	60.11
6	100	96.28

Fig. 12. Home range of bird No. 065. The contour lines contain up to 95% of the foraging areas of the bird. The isopleths were estimated using the harmonic mean transformation method of Dixon and Chapman (1980).

home range of No. 065. The last contour line corresponds with a value of 96.28 km^2. The rest of the isopleths indicate how the center of activity of No. 065 was displaced toward Patch 3. Bird No. 065 foraged in a larger area and in a more homogeneous way than No. 175, as is indicated by the more regular distribution of its data points that allowed inclusion of all points in the analysis without distorting the home range values.

Home Range of the Colony

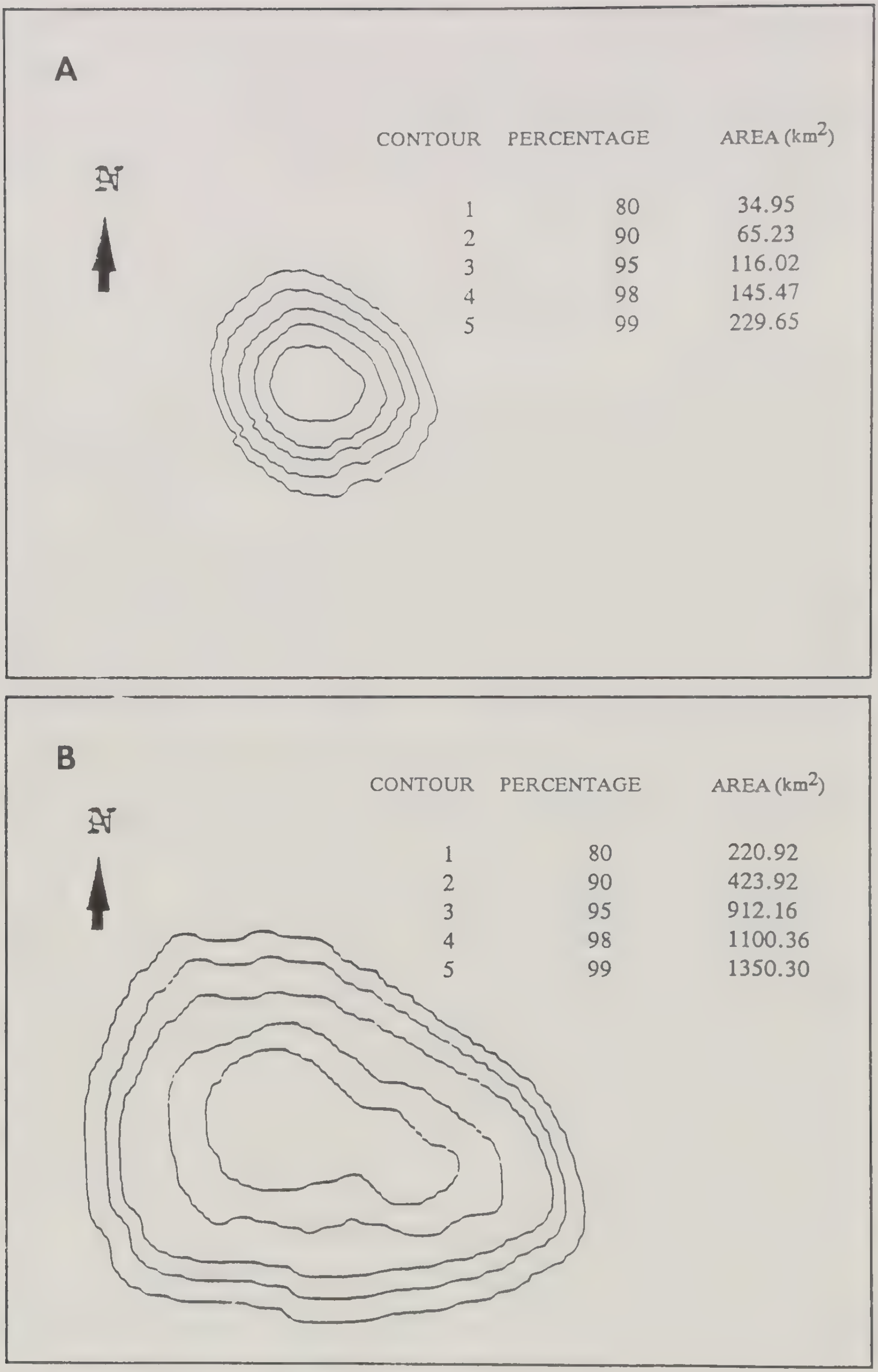
To detect seasonal change in the home range, all the data points used in the home range analysis were divided into two periods, viz., early and late breeding season. The early period includes April, May, June, and July; the late period encompasses August, September, October, November, and December. To determine both the activity center and shape of the home range, five contour lines were obtained through the harmonic mean contouring method of Dixon and Chapman (1980). The five isopleths were generated including 80-99% of the data points. The locations used in each period were independent (noncumulative) data sets. The foraging locations were also separated into different months. Each monthly data set was analyzed following the same method and the monthly changes in home range were obtained.

Not all the locations were used in the analysis because the last 5% of them were obtained at the beginning of the nonbreeding season. Although short– and long–range foraging movements during both the early and late parts of the breeding season were necessary to estimate the home range of the colony, the dispersal movements of the birds were excluded from the analysis.

Figure 13A-B indicates how the home range changed as more remote foraging places were included in the analysis. Because of the great distances of these remote places, a small increase in the number of these data points resulted in a large change in the home range. The home range of this Oilbird colony during the breeding season is not greater than 1350.3 km^2 (Fig. 13B).

Figure 13A shows that during the first part of the breeding season Oilbirds concentrated their movements in a relatively small area (229.65 km^2). The innermost contours include the activity center of the colony. The birds foraged more intensively in this area than in any other part of their range. During this period the home range did not increase at an accelerated rate.

The way Oilbirds increased their foraging area over time is illustrated in Figure 14. The home range expanded rapidly during the late breeding season from July to December. This expansion seems to be toward the southeast where, fruit was more abundant, and happened after the colony had exploited its resources around Guácharo Cave (Fig. 13B).



A

CONTOUR	PERCENTAGE	AREA (km^2)
1	80	34.95
2	90	65.23
3	95	116.02
4	98	145.47
5	99	229.65

B

CONTOUR	PERCENTAGE	AREA (km^2)
1	80	220.92
2	90	423.92
3	95	912.16
4	98	1100.36
5	99	1350.30

Fig. 13 A. Home range of the colony early in the breeding season. The analysis includes information gathered during April, May, June, and July (1988). The five contour lines were obtained using the harmonic mean transformation method of Dixon and Chapman (1980).

B. Home range of the colony late in the breeding season. The analysis includes information gathered during August, September, October, November, and December (1987-1988). The five contour lines were obtained using the harmonic mean transformation method of Dixon and Chapman (1980).

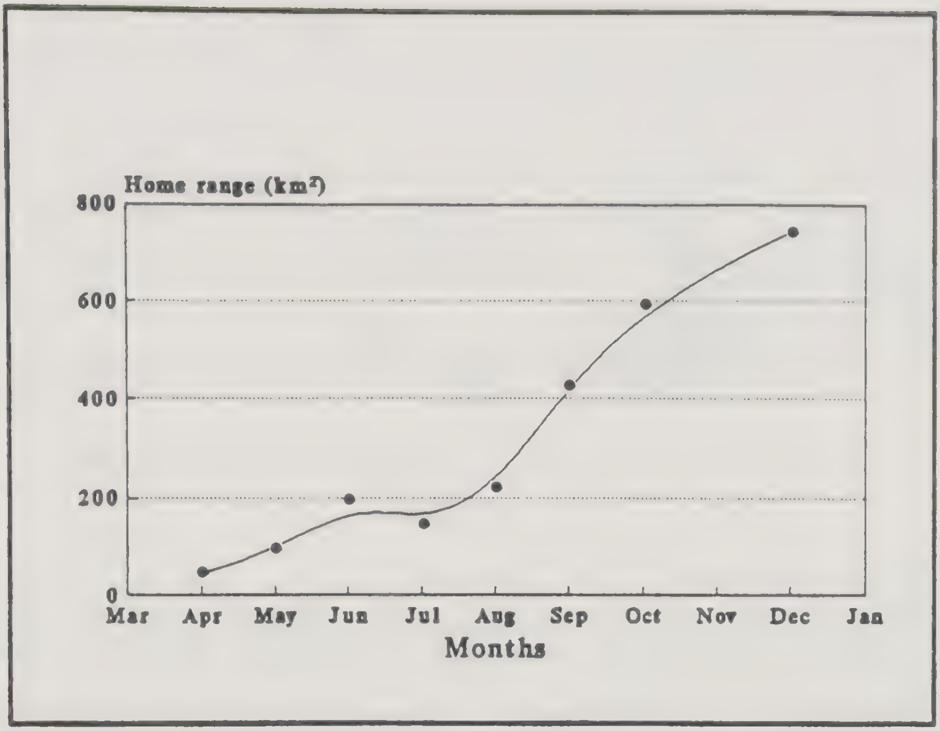


Fig. 14. Home range change during the breeding season. The figure shows monthly variations in home range values. Each monthly value was determined using the harmonic mean transformation method of Dixon and Chapman.

Early during the breeding season most of the pairs showed short–range movements. These types of foraging movements were mainly dedicated to collecting fruit for nestlings. Birds that did not return to the cave several times during the night could forage in more distant places.

At the time of the abrupt expansion of the home range, Oilbirds switched from short–range foraging movements to long–range movements. At the end of the breeding season the home range reached its maximum size and birds foraged in remote places. After this the adults and fledglings changed foraging grounds and abandoned their breeding cave.

Intensity of Habitat Use

A three-dimensional representation (Fig. 15) was constructed to show how the colony foraged in the mountainous forest from April to October. To construct the figure the home range of the colony was divided into cell grids of 3 km^2 and the

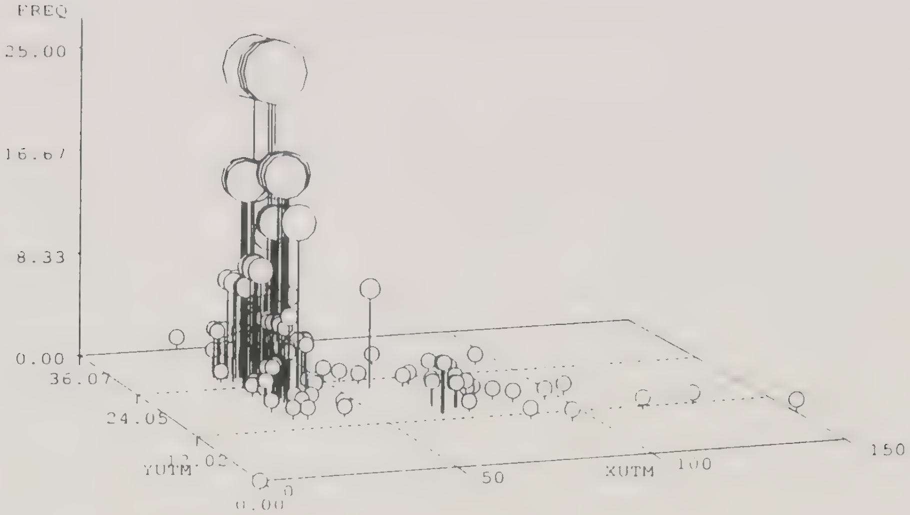


Fig. 15. Intensity of habitat use by the colony based on telemetry data collected between 1986-1988. The Y and X indicate the UTM coordinates of the study area. The Z axis shows the frequency of visits of Oilbirds to arbitrarily defined grid cells (3 km^2 each). The size of the balloons is proportional to the intensity of habitat use.

number of observations in each cell was counted. The intensity of habitat use is equivalent to the frequency of visits to the cells.

The colony showed an inverse relationship between the frequency of visits to specific places and the distance of those places to the cave (Fig. 15). Also, the colony used the habitat unevenly. Some places were visited more often than others. Some Oilbirds were observed in the same places up to 25 times during two months. Nearby foraging areas were visited repeatedly by breeding and nonbreeding birds and, as expected, breeding birds used the habitat more intensively than nonbreeding birds.

The birds foraged in the nearest patches of primary forest and then skipped the disturbed areas to forage in more remote, suitable habitats. The distances involved were 20 km or more. Disturbed habitats not only deprived the colony of resources but also forced it to forage farther. It is likely that within a frequently visited area the birds foraged on particular fruiting trees several times. The forest follows a seasonal pattern in fruit production and it is precisely at the beginning of the birds' breeding season when many food plants start to bear fruit, or already have ripe fruit. The Guácharos, therefore, have the opportunity to revisit the same fruiting tree or nearby fruiting trees as the season progresses.

Most of the feeding areas out of the center of activity of the home range are scattered toward the southeast (Fig. 13B), but the more distant southeastern places were not used intensively. In this region the birds switched from one area to another, rarely revisiting the same foraging places, with one exception. Use was most intense at Cerro El Rincon (64.00,13.00 UTM). I explored this area and set up a radio station on top of the mountain. The whole mountain is covered by *Euterpe precatoria*, one of the favored palm trees of the Guácharos. The large open space in the central rectangle of Figure 15 is the location of the town of Caripe and adjacent villages. A large area, from 0 to 12 Y UTM and from 0 to 150 X UTM, was not used by the Oilbirds. This area marks the southern end of the mountain range and the beginning of the lowlands. Here the habitat changes completely. The savanna stretches to the south and flooded plains, part of the Orinoco Delta, occur in the southeast. During the breeding season Oilbirds foraged on the mountain range but not in the lowlands.

Population Dynamics of Colony

We censused Oilbirds as they left Guácharo Cave through its only opening, counting the number of birds leaving the cave each minute during the departure of the entire colony. Counts were made simultaneously by three people. Since little light was available while counting, we restricted our censuses to nights with a full moon.

The colony size fluctuated conspicuously and showed an annual cycle (Fig. 16), although the cycles were not in phase from year to year. There were monthly differences between 1986 and 1987 in regard to the times of both dispersal and return. At the end of both years the number of individuals roosting in Guácharo Cave decreased conspicuously. A small portion of the colony stayed in the cave for two to four months. After that a massive return of Oilbirds occurred and returning individuals nested and roosted in Guácharo Cave for 5-6 months. The cycle was then repeated.

The exodus of the Guácharos occurred gradually just after the nestlings fledged. It began between the end of July and August but was most conspicuous between September and November. The dispersal of the Oilbirds showed no bias for age-class. Adults and fledglings of both sexes abandoned Guácharo Cave at the end of the year.

Two to four months were required for the birds to abandon Guácharo Cave. In 1986, 6,000 Guácharos were counted in October; the colony had decreased to 500 (5%) individuals by December. The next year the colony size decreased from an estimated 10,000 Guácharos in July to 2,700 (27%) individuals in November (Fig. 16).

Bosque (1988) reported on the postbreeding migration of Oilbirds in various Venezuelan colonies, including Guácharo Cave, as well as at Cueva Coy-Coy de Uria, northwestern Venezuela, at Los Tayos, Ecuador, and at Cueva de los Guácharos in Colombia's Cordillera Oriental.

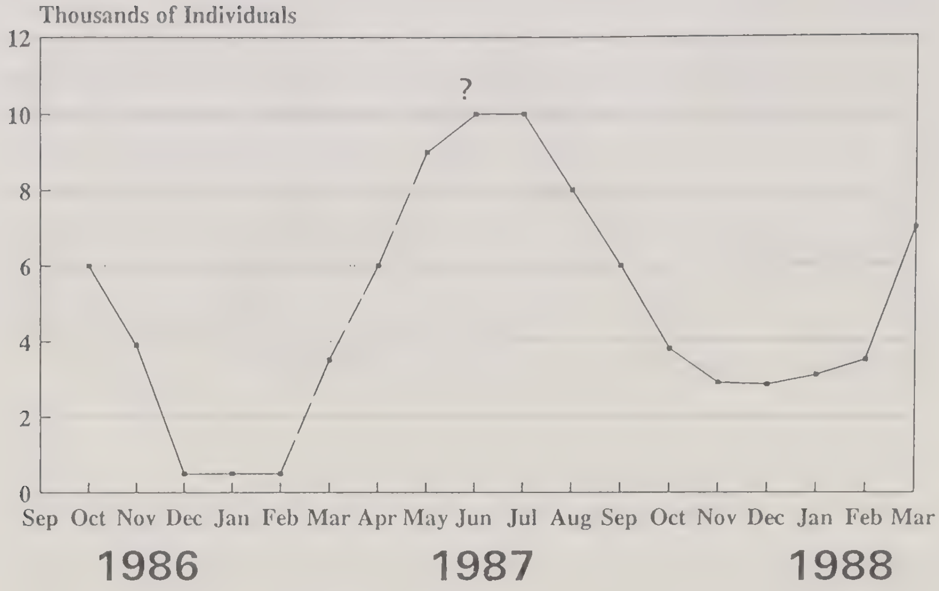


Fig. 16. Population dynamics of the Oilbird colony at Guácharo Cave, based on censuses made during 1986-1988. The solid line indicates monthly trends. The dashed line shows estimated values for times when the birds not censused. The question mark is an estimation of the colony size using census data and personal observations.

The fluctuations in colony size throughout the year corresponded with the reproductive cycle. The dispersal phase corresponded with the nonbreeding season, and the returning phase corresponded with the breeding season. Bird pairs began to mate and build, or rebuild, nests as soon as they returned to the cave. The breeding season in Guácharo Cave generally begins in March and ends in October (Ramírez, 1987).

Postbreeding Foraging

Fortunately, the Guácharos that we radio-tagged in Guácharo Cave were birds that dispersed after breeding and we were able to ascertain the direction of their departure. We took advantage of the local topography by setting up radio stations on top of the highest mountains (1,200-1,400 m) on the southeastern edge of the range. From this point we obtained a good view, free of interference, of the vast flooded plains facing the mountains. The reception thresholds were limited only by the power of our radio equipment when the weather conditions were adequate. We also double–checked the movements of birds from a temporary reception station set up on a boat in the Río Guarapiche on the edge of the flooded plains.

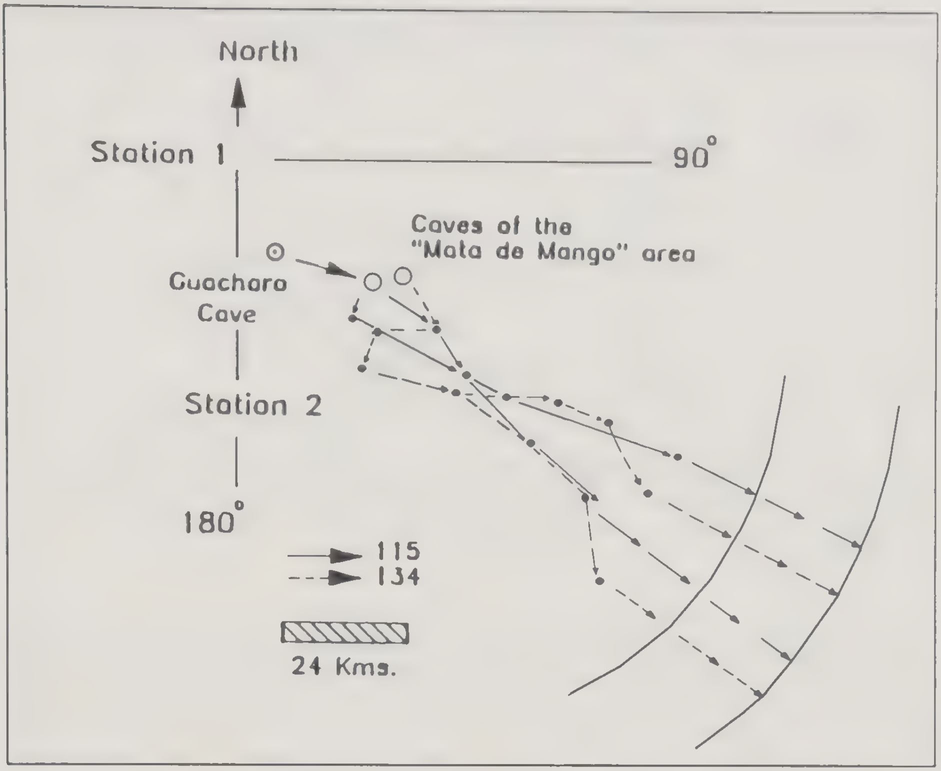


Fig. 17. Postbreeding dispersal directions of the colony from Guácharo Cave. The arrow between Guácharo Cave and other caverns indicates the dispersal direction of the colony. The figure also illustrates typical nocturnal movements of two tagged birds, Nos. 115 and 134, during the nonbreeding season. The arcs represent reception thresholds from Stations 1 (Cerro Negro) and 2 (Cerro El Rincon).

Here we not only received the signals of birds passing nearby but also saw numerous Oilbirds flying above the canopy of the flooded forest going southeast. Unfortunately, we could track the birds for no more than five minutes due to poor reception.

Oilbirds dispersed to the southeast, about 24 km from Guácharo Cave, to another cavern system in the region, Mata de Mango (Fig. 17). The Mata de Mango area is a limestone mountain range covered by pristine tropical forest. Deep canyons, rivers, waterfalls, multiple caverns, and sinkholes are common in the region. These mountains are nearly inaccessible due to the irregular topography. Not without difficulty, we confirmed the presence of unknown roosting sites by exploring some of the caves and locating radio signals of tagged birds. The birds also switched foraging grounds (postbreeding dispersal) and obtained fruit from an entirely different habitat, mainly outside the boundaries of the mountain range. Now they foraged in the extensive flooded plains of the Orinoco Delta. To

Table 4. Postbreeding roosting caves of the same Oilbirds that had bred in Guácharo Cave.

Bird No.	Dispersal Date	Cave Name
115	15 Oct. 1986	Cueva Grande de Anton Goering
134	06 Oct. 1986	Cueva Clara
275	06 Oct. 1986	Unknown (?)
235	15 Oct. 1986	Sima de los Gonzalez
175	19 Aug. 1987	Cueva Grande de Anton Goering
195	29 Oct. 1987	Sima Bastimento 1 y 2
214	30 Oct. 1987	Sima Bastimento 1 y 2

Caves mentioned in table have been explored by the Venezuelan Society of Speleology (Sociedad Venezolana de Espeleologia 1974a, 1974b, 1975, 1976, 1982). All caves occur in Mata de Mango area (63°27' – 63°11' W x 10°19' – 10°01'30"N).

reach their remote foraging grounds, the Oilbirds had to fly a round trip of at least 240 km every night. Each night the birds averaged 10 hours outside their caves. The Guácharos foraged and dispersed toward the same area during both years of the study (Table 4).

From Stations 1 and 2 we tracked the birds and saw an entirely different set of nocturnal movements from those recorded during the breeding season. Oilbirds Nos. 115 and 134 illustrate the foraging movements on a typical night (Fig. 17). The birds left the caves early in the evening, as usual, and turned southeast. Instead of foraging in the vicinity of the caves, they flew southeast and crossed the first reception threshold. Almost an hour later they crossed the second reception threshold; after that their signals became less audible until we lost them in the same general direction. The birds stayed out of our range most of the night; between 0230 h and 0330 h they returned to our reception space, traveling to their caves along the same general pathway as their departure route. All the birds showed a significant preference for the southeastern foraging grounds of the Orinoco Delta. Figure 18 shows the frequency distribution of the bearings of all the tagged birds that we obtained from the Cerro El Rincon station. The data presented correspond with the trajectories of the birds as they passed the first threshold of reception.

Each bird exhibited a specific preference for a foraging direction ($X^2 = 805.50$, df = 17, a = 0.001). Most of the bearings were between 90° and 130°, with an average direction of 106.52° (Table 5).

The bearings had a unimodal distribution. Most of their mean directions were similar, ranging from 96.53-109.68° (Fig. 19). All presented relatively low standard deviations, indicating a strong preference for certain areas in the flooded plains. Only Bird No. 235, as shown by its mean, foraged away from the rest. This

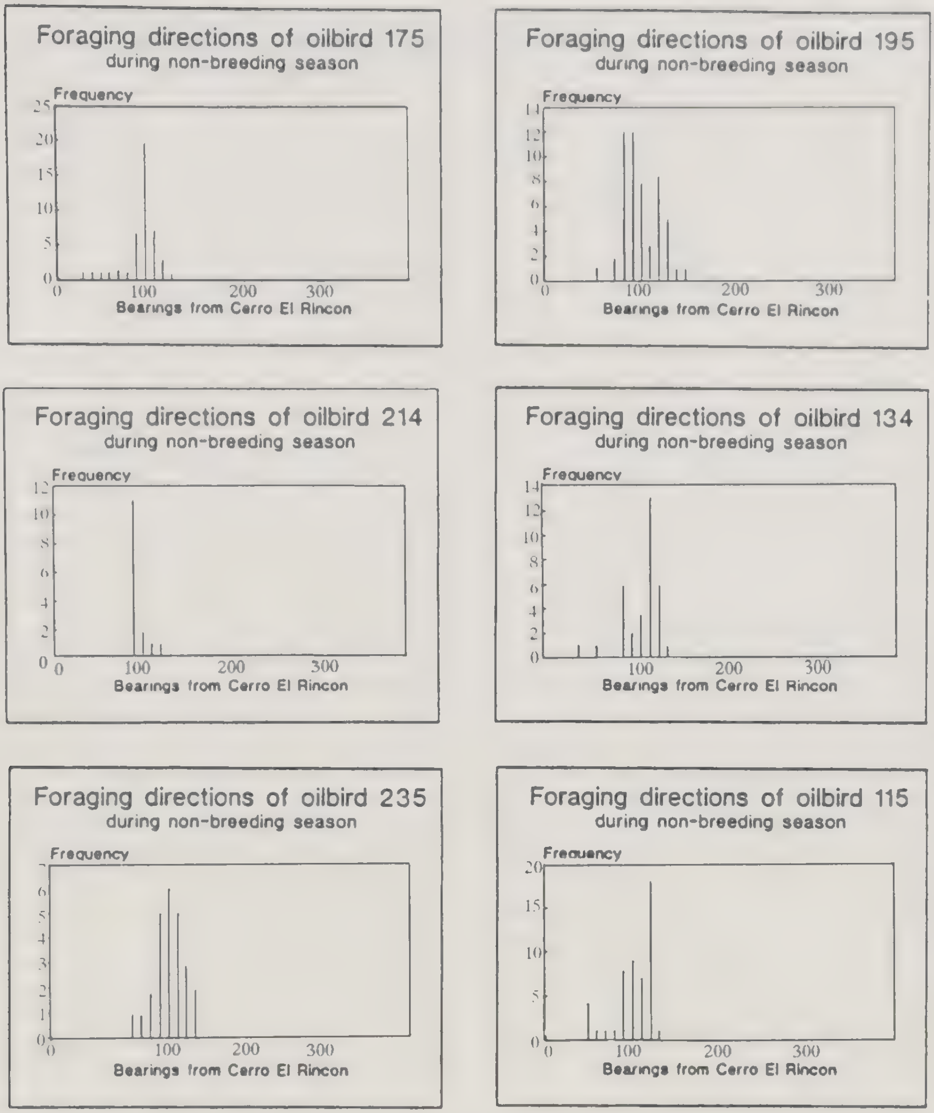


Fig. 18. Histograms of the departure directions of foraging birds Nos. 235, 115, 134, 214, 195, and 175 during October-January 1986-1988. The bearings were grouped in 10° arcs. The data were collected during the first three hours after the birds left Mata de Mango caves.

bird also displayed a nonrandom foraging direction, oriented toward the flooded plains.

The birds showed a significant nonrandom homing direction as they returned to their caves ($X^2 = 951.39$, df = 17, a = 0.001). The frequency distribution of their return movements showed a high degree of overlap and similarity to their departure directions, indicating that Oilbirds might follow the same route when leaving from and returning to their caves.

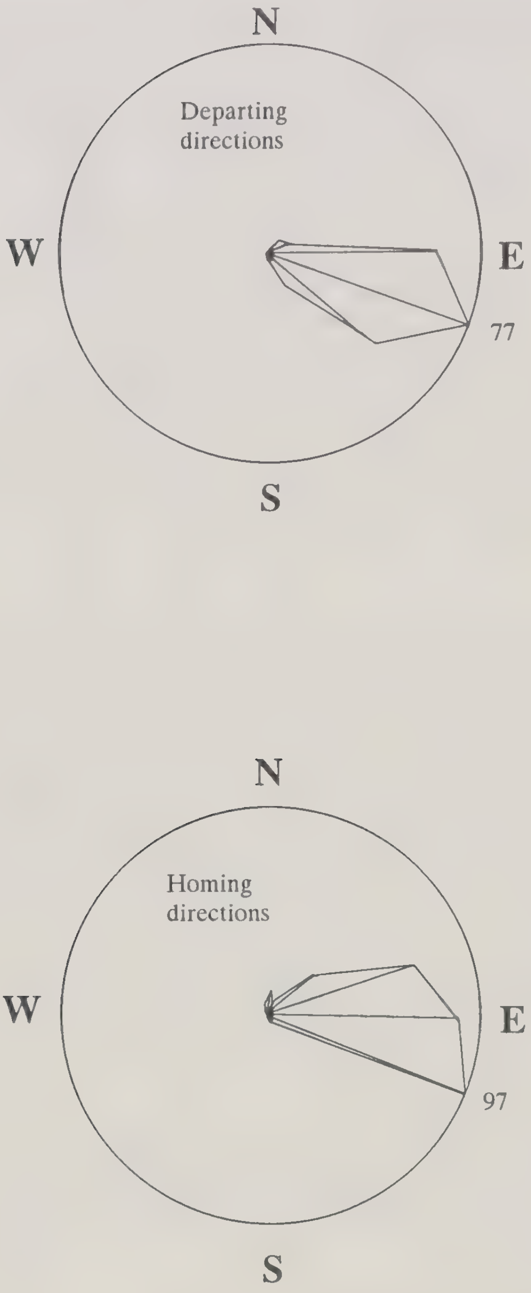


Fig. 19. Grouped data indicating departure foraging directions, homing directions, and frequencies for six tagged birds (Nos. 115, 134, 175, 195, 214, and 235) between September-January 1986-1988. The length of each line within the circle indicates absolute frequency of bearings. The highest frequency is represented by the radius (e.g., 77 in the figure of departure directions). The bearings were grouped in ten degree arcs. The bearings were obtained from Cerro El Rincon. Most of the bearings for homing directions were obtained between 0230 h and 0545 h.

Table 5. Means and standard deviations of the frequency distributions of the departure bearings of Oilbirds in caves of Mata de Mango.

Bird No.	**No. Observ.**	**r**	**Mean angle (degrees)**	**S. D. (degrees)**
134	34	0.941	109.6	19.5
195	54	0.940	109.5	19.7
214	15	0.990	96.5	8.0
235	25	0.956	130.3	16.8
115	50	0.936	101.2	20.3
175	46	0.933	96.7	20.8
All birds	224	0.929	106.5	21.5

Values in table obtained from the frequency distributions of bearings of Fig. 18.

There was an exceptional situation during the nonbreeding season of 1986. Bird No. 275 departed from Guácharo Cave but we never obtained its signal again, although we did with the remaining birds. There are several likely explanations. The bird died deep inside a cave of Mata de Mango, where its signal could not be heard, it died in a deep canyon, also where the signal was inaudible, it traveled an even greater distance to a cave in another state, or the transmitter failed. Because the bird was healthy and strong when captured, I suggest that this bird migrated out of Monagas State.

7

DIET

Seasonal Trends in Diet

We selected 10 solitary nesting pairs along Humboldt's Gallery to study feeding activities. The nests were located in three sections of the cave. Three nests were close to the end of the gallery, about 750 m from the entrance. Four nests were about 500 m from the entrance, and the other three were about 400 m from the entrance. We also selected pairs according to their brood size. Nests with none, one, two, and three nestlings were chosen.

In order to obtain seeds regurgitated in the cave by either nestlings, parents, or both, we set seed traps under each of the nests, following the Snows' (1978) method. The seed traps, 1 m x 0.6 m, were built of wire mesh. Nailed to the wall, they looked like hanging trays. These collected at least 95% of the regurgitated seeds. Traps were emptied daily for 3 or 4 days each week, until the nestlings fledged and the family abandoned the nest. At the same time collections were made, nestlings were weighed and measured. The seeds were stored in labeled plastic bags with date, hour, and nest number. Each seed sample was weighed, counted, and assigned to a typological classification using a previously prepared seed catalog. During the study period whole, fresh, ripe fruits were also collected either in the cave (dropped by the birds) or in the forest. To detect temporal changes, the information gathered was grouped by month and year. Species occurring in low abundances were excluded from the figures.

The seeds were examined and identified by Carlos Bosque from the Simón Bolívar University in Venezuela. Dr. Bosque is presently studying the phenology of the food plants of Oilbirds in the Caripe area.

There were monthly and yearly differences in the number of fruit species, the number of food items in the diet, and the diversity of species brought to the cave (Table 6). Although a higher proportion of the seeds was secured in 1987, based on Shannon's diversity index, the sample from 1987 was less diverse than that from 1988. There was a difference of nine species between the two years. The shorter sampling period in 1987 (two months) could have affected this result. Data from 1987 showed a lower equitability index value, indicating that most of the species were less evenly represented in the samples than in 1988.

Each plant species was assigned a number from 1 to 40. Table 7 lists the species and shows their relative abundance for the combined two years. Twelve of 18 species of laurels, and five of seven species of palms were identified to species.

Table 6. Quantitative parameters of the diet of nestlings, 1987-1988.

Date	No species	No. items	H-index*	J-Index*
1987: July	22	15,822	1.113	0.051
Aug.	12	2,756	1.042	0.087
Combined July-Aug.	22	18,578	1.106	0.050
1988: May	18	2,719	1.935	0.108
June	17	5,791	2.060	0.121
July	20	5,171	1.962	0.098
Aug.	9	1,767	0.625	0.069
Combined May-Aug.	31	15,448	2.225	0.072
Combined 1987-1988	40	34,026	1.969	0.049

* H-index is Shannon's diversity index. J-index represents Shannon's equitability index.

Only one species, *Dacryodes trinitensis*, is a member of the family Burseraceae. The remaining 14 species are not yet identified. Laurels and palms made up 62.5% of all plants in the diet. Laurels comprised most of the food items (51%) and were the most diverse component of the nestling Oilbird's diet. Palm trees were second in order of importance (31%). *Dacryodes trinitensis* (Burseraceae) held the third position due to its relative abundance (7.6%).

The most abundant species brought to the cave by the Oilbirds were *Persea coerulea* and *Geonoma densa*. The skewed distribution in the food items toward just two species resulted from only two months of sampling in 1987. In July 1987 most of the seeds were *Persea coerulea* and *Geonoma densa*.

Monthly Fluctuations in Food Items

Figures 20-22 show some monthly changes in the abundance of the most important Lauraceae and Palmae species. Species of Palmae were gradually substituted by species of Lauracea. In May more than 80% of the species were palms but in August laurels were most abundant in the seed traps (Fig. 20). The fruits carried to the cave by Oilbird pairs reached a peak of abundance and species richness between June and July. By August the number of species in the diet decreased abruptly by almost one half (Table 6).

Variation in the abundancy of the plant species followed a substitution pattern in which top–ranking species were replaced from month to month by emerging species. Species occupying low positions in the rank of abundance reached their maximum numbers in the samples and then declined gradually (Figs. 21, 22).

Table 7. Relative abundance of the 40 species of food plants found in the cave.

Family		Percentage
Lauraceae		51.0
1.	*Ocotea floribunda*	5.1
2.	*Persea coerulea*	33.0
3.	*Phoebe cinnamonifolia*	6.7
4.	*Nectandra aff. laurel*	2.1
5.	*Beilschmedia sulcata*	<1.0
6.	*Nectandra sp. 1*	<1.0
7.	*Nectandra turbacensis*	<1.0
8.	*Nectandra sp. 2*	<1.0
9.	*Nectandra membranacea*	<1.0
10.	*Ocotea aff. austini*	<1.0
11.	*Nectandra sp. 3*	<1.0
12.	*Nectandra sp. 4*	<1.0
13.-18.	*Unidentified species*	<1.0
Palmae		31.0
19.	*Bactris setulosa*	<1.0
20.	*Jessenia bataua*	<1.0
21.	*Geonoma densa*	25.7
22.	*Euterpe precatoria*	7.6
23.-24.	*Unidentified species*	<1.0
25.	*Prestoea acuminata*	6.9
Burseraceae		7.6
26.	Dacryodes trinitensis	7.6
Unidentified		
27.-40.		10.4

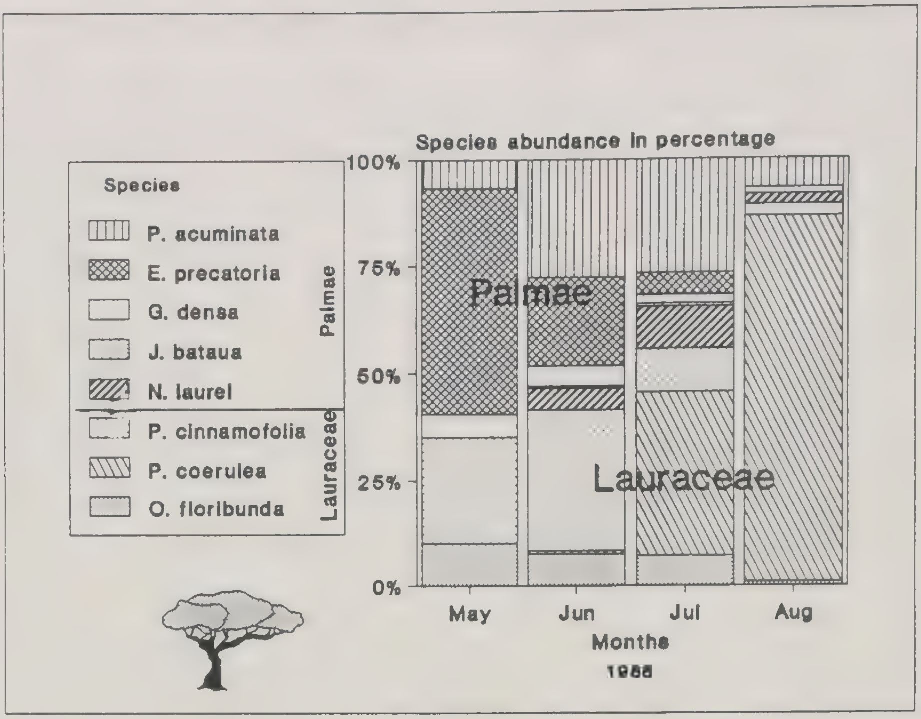


Fig. 20. Monthly fluctuations in the percentages of eight important species of Palmae and Lauraceae found in the seed traps in 1988. The figure also shows a substitution pattern between both families.

Figures 21 and 22 show the monthly change in relative abundance of each food found in the seed traps. Between July and August 1987 there was a marked reduction, of about 6,000 seeds, in the abundance of *Persea coerulea* (no. 2) and *Geonoma densa* (no. 21) in the diet. These two species comprised about 90% of all the food items.

At the beginning of the breeding season in May, four species out of 18, *Euterpe precatoria* (no. 22), *Dacryodes trinitensis* (not shown in Fig. 22), *Nectandra aff. laurel* (no. 4), and *Phoebe cinnamonifolia* (no. 3), were abundant in the diet. The next month, different species, e.g., *Ocotea aff. austinii* (no. 10), appeared in the diet. The absolute frequency of items of some species in May increased whereas some others decreased. *Euterpe precatoria* declined from the top in the abundance to 8.94%, *Phoebes cinnamonifolia* rose to the top, increasing from 12.57% to 22.15%. *Prestoea acuminata* (no. 25) rose from 3.42% to second in rank with 18.78% followed closely by *Dacryodes trinitensis*. *Nectandra aff. laurel* dropped from 16.91% to 3.52%. A laurel tree, unidentified species no. 16, not recorded in May, rose to the fourth place in the abundance rank.

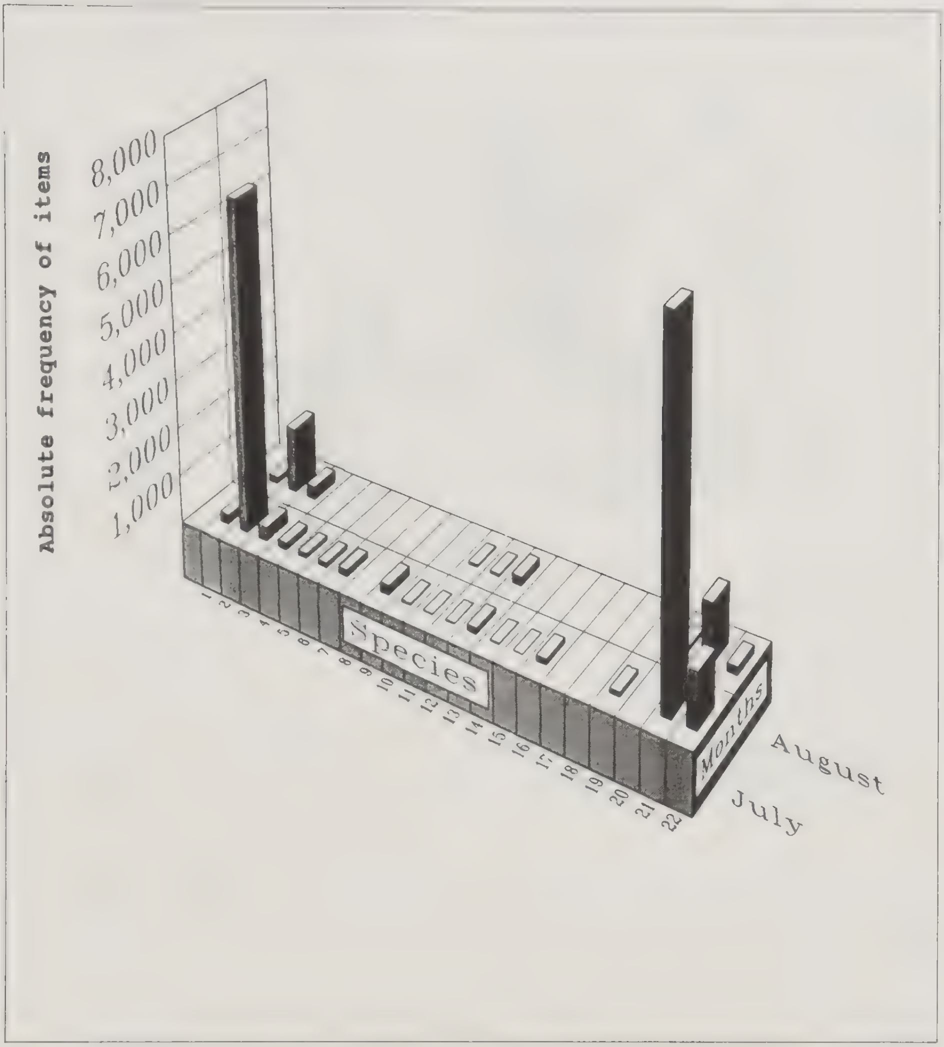


Fig. 21. Variations in the number of seeds of Lauraceae and Palmae species found in seed traps July-August 1987. Species numbers correspond to those listed in Table 7.

In July *Phoebe cinnamonifolia* was almost substituted by *Persea coerulea*. Some species, such as *Nectandra* species 4 (no. 12) appeared for the first time in low numbers but most of the species in June showed a marked decline in abundance. In August *Persea coerulea* comprised 85% of the nestlings' diet; many of the species previously present had vanished. The proportions of the remaining species were reduced substantially.

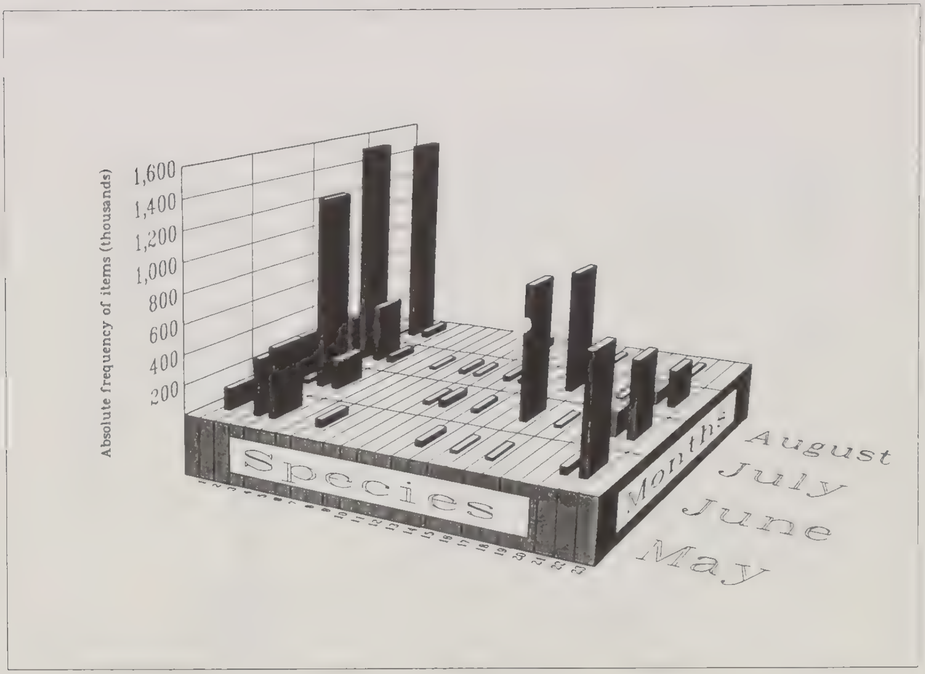


Fig. 22. Variations in the number of seeds of Lauraceae and Palmae species found in seed traps May-August 1988. Species numbers correspond to those listed in Table 7.

Seasonal Availability of Fruit in Caripe Area

Tracking Oilbirds required numerous incursions into their remote feeding area where, between March and October, we were able to observe the presence or absence of fruit on their food plants. We also noted general seasonal phenology through the year. These observations were restricted to the trees found along ten hiking routes which served as long transects, averaging 1 km, distributed within the study area. Because of the heights of the trees, it was difficult to determine presence of fruits at the early stages of fruit development; palms 5–10 m high were easier to observe than trees 10–20 m high.

We obtained only partial qualitative information about phenology. There is no literature on the seasonality and availability of fruit occurring in the Caripe Mountain range; although Carlos Bosque, from Simón Bolívar University, is conducting phenological surveys of the area with the double goal of identifying the Oilbird's food plants and as well as characterizing the phenology of these plants. His preliminary results have complemented and reinforced my field observations indicating a marked seasonality in fruit production in the study area.

The eight plant species observed in the field showed a seasonal pattern in fruit

Table 8. Presence or absence of ripe fruit in eight species of Lauraceae and Palmae.

Species	Mar.	Apr.	May	June	July	Aug.	Spet.	Oct.
E. precatoria	x	x	x	x	x	x	x	—
B. setulosa	?	x	x	x	x	x	x	—
G. densa	?	?	x	x	x	x	x	—
O. floribunda	?	?	x	x	x	x	x	—
P. coerulea	?	?	?	x	x	x	?	—
P. cinnamonifolia	?	?	x	x	x	x	?	—
N. laurel	?	?	x	x	x	x	?	—
D. trinitensis	?	?	x	x	x	x	x	—

x: presence of ripe fruit; ?: not determined (possible absence); –: absence of ripe fruit.

production (Table 8). A conspicuous dry season occurs in the area between December and March, during which time most of the trees are flowering and bear unripe fruit. These species are shown with a question mark in Table 8.

The fruiting time coincides with the wet season at the end of March. The number of species bearing ripe fruit peaks between June and July. *Persea coerulea*, *Phoebe cinnamonifolia*, *Dacryodes trinitensis*, and possibly *Prestoea cuminata* are the most plentiful species in the mountainous forest (Table 8) and are then included in the Oilbird diet.

Between August and September there is a sharp decline in the number of species bearing ripe fruit; *Persea coerulea*, *Geonoma densa*, and *Euterpe precatoria* are among the most important species with fruit at this time (Figs. 21, 22) and are also most abundant in the diet. The decline in the availability of fruit coincides with, and possibly determines the end of the Oilbird's breeding season.

Possibly both the number of fruiting species and the fruiting peak change from year to year (Table 6; Figs. 21, 22). It is well known that tropical seasonal environments present a complex phenology with many abiotic and biotic factors influencing the spatio-temporal abundance of fruits (Frankie, et al., 1974; Wheelwright, 1986; Fleming, et al., 1987; Primack, 1987; Fleming, 1988).

Does the fruit diet of the Oilbird epitomize selective feeding, or does the abundance of diverse species in its diet simply reflect the abundance of fruit in the forest? Oilbirds do not forage on all the possible fruit produced in the forest, selecting canopy fruit as opposed to understory fruit. Oilbirds could be considered selective foragers in a general sense, as Snow (1962) suggested. Within the set of plant species that comprise the nestlings' diet, it is not certain that a particular species appears in the diet as soon as its fruit becomes available. It is not feasible to know about the availability of food resources in the environment solely based on an animal's diet. In Trinidad, a less seasonal habitat, Oilbirds forage on 36 species, exhibit year to year similarity in their diet, and seem to forage on fruit as it becomes available (Snow, 1962). The monthly fluctuations of the Oilbird's food plants in Caripe suggest that Oilbirds capitalize on the fruit as it becomes available. Because of the lack of extensive phenological information, this issue must be approached carefully. The birds could also show, for a short period, some degree of fruit selectivity (see p. 56).

Characteristics of Fruit Consumed

Fruit was analyzed to evaluate the components affecting the Oilbird's use of particular species and its value as a food. Nine representative species of fruit were analyzed for protein, ash, water content of pulp or aril, edible part of the fruit, seed burden, relative yield, and energy content. These were chosen because of their abundance in the forest and because, presumably, they were most commonly consumed by the Oilbirds. The ripe fruit was frozen and kept in dry ice for future analysis. Dried fruit samples were analyzed at the fibre laboratory of Cornell University. For an extensive explanation of the various methods involved in fruit analysis see Van Soest and Robertson (1985).

The seed burden, expressed as the fraction seed mass/fruit mass, (Ws/Wf), gives a measure of the amount of ballast Oilbirds ingest after they swallow the fruit whole. Oilbirds neither damage nor digest the seeds, thus the seeds become useless extra bulk that reduces the volume available for more fruit. They must egest the seeds quickly either through regurgitation or defecation, or both.

The "relative yield" (RY), a concept introduced by Herrera (1981), is a measure of the amount of dry nutritious material obtained by a frugivore as a function of the number of seeds per fruit (n), the fresh weight of a single seed (s), and the fresh weight of the aril or pulp (P).

$RY = (1 - W)/(1 + ns/P)$, where W is the proportion of water content of the aril.

The amount of dry, mostly nutritive matter, expressed as a percentage of the whole fruit weight, is not a realistic measure of the value obtained from eating a fruit. The edible dry aril includes indigestible carbohydrates, e.g., cellulose, lignin, cutin, and ash, that are made of nutritionally unavailable minerals such as silicates (Van Soest and Robertson, 1985). Herrera (1981) introduced the overall profitability factor (OP) as a way to incorporate the chemical components (d), e.g., lipids and proteins, and the design component (RY) of a fruit into a single parameter. OP is a more realistic estimation of the food value of a fruit.

$OP = RY \times d$, where d is expressed in terms of the percentage of some valuable nutrient.

Table 9. Relative yield (RY) of some species of Lauraceae, Palmae, and Burseraceae whose seeds were collected in the cave.

Species	WFM (g)	SM (g)	% Water	PM (g)	RY
Lauraceae					
O. floribunda	5.80	2.09	60.98	3.71	0.250
P. coerulea	0.64	0.38	46.88	0.26	0.216
P. cinnamon	0.62	0.27	64.52	0.35	0.200
N. aff. laurel	1.58	0.79	57.68	0.79	0.211
B. sulcata	12.00	4.08	60.23	7.92	0.262
Palmae					
B. setulosa	5.32	3.99	47.11	1.33	0.132
J. Bataua	16.25	6.21	41.78	10.04	0.359
E. precatoria	1.29	0.61	49.57	0.68	0.265
Burseraceae					
D. trinitensis	2.51	1.48	73.75	1.03	0.107

WFM: whole fruit mass; SM: seed mass; PM: pulp mass. Sample size = 14 examples of each species.

The OP values in Table 9 were obtained by including the addition of percentages of proteins, lipids, and digestible carbohydrates of the fruit pulp in the parameter *d*.

Accumulated monthly values of overall profitability and energy (Kcal) were obtained using the attributes of the most important species of fruit of the families Lauraceae, Palmae, and Burseraceae. These monthly values were estimated by multiplying the specific OP value times the number of examples of a given species that were recovered. The accumulated OP values for each species were added. The method allows an analysis of how monthly changes in fruit abundance affect total fruit profitability. The monthly OP values were plotted along with the accumulated enery (Kcal) and the number of fruit for that month.

All fruit collected by Oilbirds for their nestlings are canopy fruit produced in large quantities; all have a single seed and a relatively thin nonsucculent aril.

The components of the different fruit vary (Tables 9, 10). In the Lauracea, 44% of fruit weight is due to the seed, the pulp averages 58% water and 42% edible (dry) aril. On the other hand, in palm fruit the seed averages 53% of the whole weight, while the pulp contains 46% water and a higher fraction of edible aril (54%). The differences between families in the weight of the edible aril is due to the amount of water. Lauraceae and Palmae fruits showed similar mean OP values

Table 10. Overall profitability (OP) of some species of Lauraceae, Palmae, and Burseraceae whose seeds were collected in the cave.

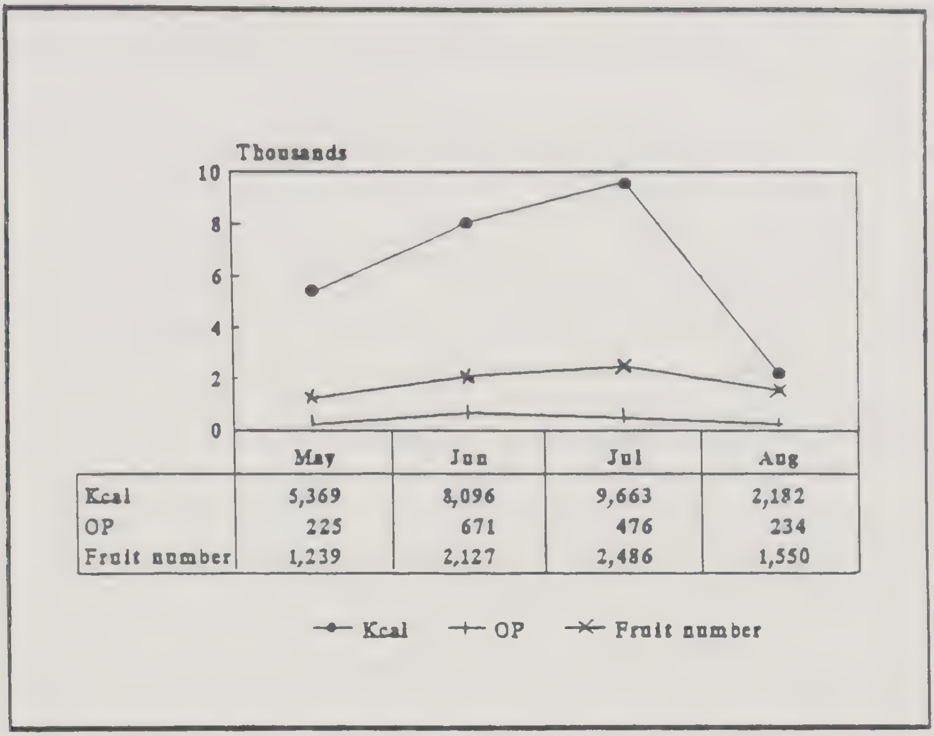
Species	% Protein	% Ash	% Carb + Lipds	OP
Lauraceae				
O. floribunda	6.53	2.35	71.00	0.194
P. coerulea	10.92	1.63	54.83	0.142
P. cinnamon	16.23	5.32	56.29	0.145
N. aff. laurel	7.44	3.54	71.39	0.166
B. sulcata	6.54	2.22	65.29	0.188
Palmae				
B. setulosa	8.57	3.83	15.91	0.032
J. Bataua *	7.40	nd	92.60	0.359
E. precatoria	6.76	2.38	16.16	0.060
Burseraceae				
D. trinitensis	6.32	5.78	24.82	0.033

* Values from Balick and Gershoff (1981). Sample size = 14 examples of each species.

(0.167, and 0.150 respectively). Lauraceous fruit is slightly more profitable than palm fruit because it is smaller and lighter. *Dacryodes trinitensis* (Burseraceae), like palm fruit, is high in indigestible carbohydrates and nutrient composition. The differences lie in the exceptional light weight of this fruit in relation to its size, and in that more than 70% of its weight is water.

The morphology as well as the nutrient composition of fruit in the Oilbird's diet were analyzed by Snow (1962) and White (1974). They found the average nutrient composition of fruit, based on the weight of dried arils, to be protein 12%, lipid 32%, and carbohydrate and ash 56%. Fruit contains an average of 5.55 kcal/g. These fruits, in contrast to nonsucculent fruits, have a high lipid and protein content. The amount of water in succulent fruits is very high (75–85%) making them less nutritious. Palm fruits eaten by Oilbirds have between 45–50% water in their arils, 9% protein, 20.5% lipids, and 58.5% carbohydrates and ash (Snow, 1962).

Figure 23 shows an increase in the total OP, energy, and amount of fruit delivered to the nestlings during May and June. In June the OP value peaked and then decreased in July and August. The amount of fruit and its energy value decreased after peaking in July. The results suggest that Oilbirds brought to their nestlings higher quality fruit the first two months of the breeding season. Between June and July the overall profitability was inversely correlated with the quantity



	May	Jun	Jul	Aug
Kcal	5,369	8,096	9,663	2,182
OP	225	671	476	234
Fruit number	1,239	2,127	2,486	1,550

Fig. 23. Changes in total energy content of fruit, overall profitability (OP), and amount of fruit delivered to the nests each month during the breeding season, 1988. The figure shows data for the nine most abundant species of Lauraceae, Palmae, and Burseraceae.

of fruit and its energy content. The results raise the question of fruit selectivity versus availability. Oilbirds could be selective foragers mainly the first two months (May and June) of development, which are critical for the nestlings (see p. 62). This, however, is speculative.

8

GROWTH RATES

Growth rates of birds are currently seen as the result of complex selective processes for breeding (Ricklefs, 1968, 1969, 1976; O'Connor, 1984). The pattern of growth in the Oilbird has received considerable attention among biologists (White, 1974; Ramírez, 1987). This bird has one of the lowest rates of growth among all birds in both temperate and tropical environments (Ricklefs, 1976). Perhaps the low rate of growth is a consequence of the frugivorous diet (Snow, 1962; Ricklefs, 1968, 1976; Morton, 1973; White, 1974).

In this study 20 nestlings in ten nests were weighed and measured regularly throughout their development. An average growth curve was obtained by pooling the measurements of 13 nestlings; seven nestlings were not included because they died during the first month.

All growth data were curve-fitted following Ricklef's method (Ricklefs, 1967). Briefly, the data are first expressed as a proportion of the asymptotic weight value. Then the values are transformed to conversion factors (see equations in Ricklefs, 1967) and plotted against age. A posteriori iteration process determines which growth equation, i.e., logistic, Gompertz, or von Bertalanffy, produces the straightest line. The slope and the consant **K** are estimated from this line. The slope of the line is the slope of the equation at its point of inflection, **dW/dt**. Values of **dW/dt** and **K** are important because comparisons can be made between growth curves fitted by the same equation. The differences among the three growth equations lie in their inflection points. They occur when 50, 37, and 30%, respectively, of the asymptote value is attained. Maximum growth rate occurs earlier in the Gompertz and von Bertalanffy curves than in the logistic curve.

The mean weight and its standard deviation was calculated according to the age of each nestling. This method yields not only an average growth curve but also explains variances around the mean weight. Only the first sixty days of development were included in the analysis. After this period young Oilbirds lose weight and fledge.

The data on the growth of ten nestlings, which presented the most extensive data set, were compared with the amount of food (determined by the weight of the seeds collected at the nest) brought to the nests. The weight of the seeds is a good indicator of the parental effort. It also reflects variations in the amount of fruit pulp brought to the nests. The average seed and fruit pulp ratio is close to 1.1 in terms of weight. As an average, seeds constitute 42% of the weight of the whole fruit (Table 11).

The growth rate of the nestlings fits best the logistic equation (Fig. 24, Table

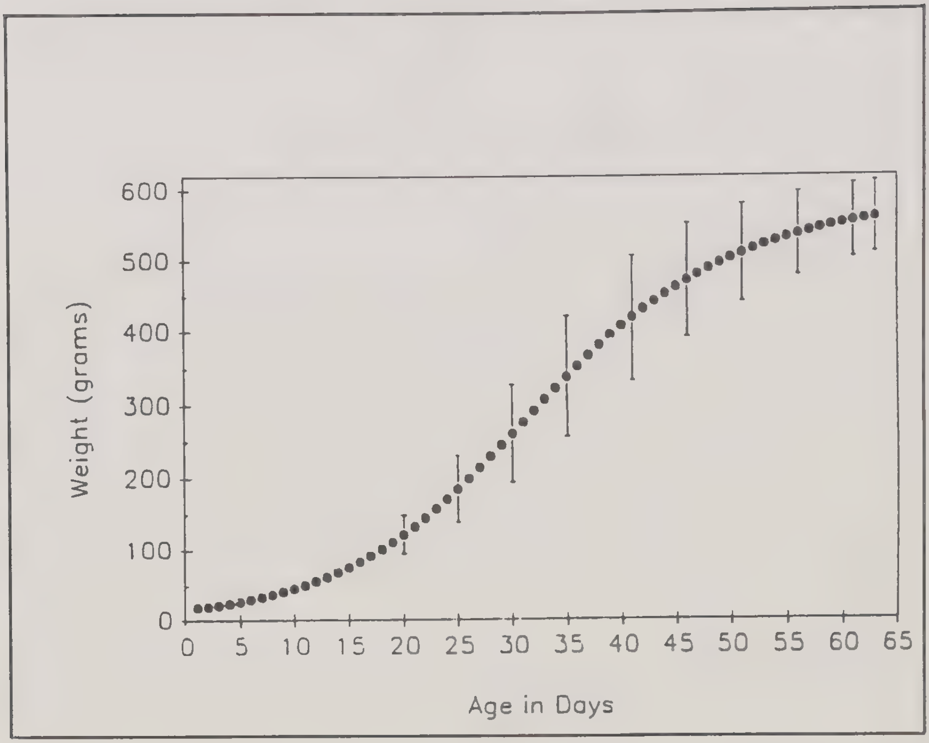


Fig. 24. Average growth curve of Oilbird nestlings. The curve was obtained using Ricklef's (1967) curve fitting method.

12). The rate is relatively low the first two weeks, then it becomes exponential. During the first month nestlings gain an average of 260 grams, 70% of this is gained in the third and fourth weeks. The maximum growth rate is reached at 30 days of age (the inflection point), after which weight increases at a slower rate until the asymptotic region of the curve is reached (560 grams).

To grow from 10% to 90% of the asymptotic weight [$t_{10\text{-}90}$ (days) = 4.4/K (Ricklefs, 1967)] requires 44 days. Oilbirds showed **K** = 0.108. This value is low when compared to **K** values of smaller, passerine, birds such as the Blue-gray Tanager (*Thraupis episcopus*) (**K** = 0.276), Clay-colored Robin (*Turdus grayi*) (**K** = 0.44), and Yellowed-bellied Seedeater (*Sporophila nigricollis*) (**K** = 0.604), which reach their asymptotic weight at between 7-16 days (Ricklefs, 1976).

In contrast to the **K** value of 0.108 given above, Ramírez (1987) reported a value of 0.100, obtained from the measurements of the nestlings in 149 nests in Guácharo Cave. Intraspecific variation in **K** values among Oilbird colonies, or among broods with the same colony, may reflect changes in environmental conditions. The coefficient of intraspecific variation (100 x sd/mean) introduced by Ricklefs (1976), between the Guácharo colony and the Trinidadian colonies

Table 12. Properties of growth equations. The table shows the parameters of three different growth equations, logistic, Gompertz, and von Bertalanffy. After Ricklefs (1967).

Cummulative Growth (w)	Logistic	Gompertz	von Bertalanffy
	$\frac{a}{1\text{-be-}^{Kt}}$	$_{ae}\text{-be-}^{Kt}$	$a(1\text{-be}^{Kt})^3$
Absolute Growth rate (dW/dt)	KW (1-w)	-KW ($\log_e$W)	#KW$^{2/3}$(1-W$^{1/3}$)
Relative growth rate (1/W.dW/dt)	K (1-w)	-K ($\log_e$W)	-3K (1-W-$^{1/3}$)
Inflection point (Wi)	1/2 (0.50)	1/e (037)	S/27 (0.30)

W is weight of growing organism, *a* final weight (asymptote) achieved, *K* a constant which is proportional to overall growth rate, *e* base of natural logarithms, and *b* a constant which translates the time axis such that time *t* is equal to zero at inflection points where $b = 1$ for the logistic and Gompertz equations, and $b = 1/3$ for the von Bertalanffy equation (after Ricklefs, 1967).

is 8.56% (sd = 0.008, mean = 0.101). It seems to be that Guácharos in Venezuela grow slightly faster than their conspecifics in Trinidad. Perhaps this is related to the availability of fruit and the differences in seasonality, as Trinidad is less seasonal than the northeastern mountain range of Venezuela.

The nutrient composition of nestling tissue changes relative to the growth pattern (White, 1974). In the first month the nestling corporal components are 68% water, 9.25% protein, and 18% lipids. During this period the daily rate (grams/day) of obtained proteins and lipids shows a ratio of 1:2 respectively (White, 1974). For each gram of protein incorporated in the tissues two grams of lipids are stored as accumulated fat.

In the second month, when they reach their asymptotic weight, the components are 59% water, 27% lipids, and 11.25% proteins. At this time, particularly between 40–45 days of age, the daily rate of protein lipid accumulation shows a ratio of almost 1:3 (White, 1974).

During the third month of development nestlings lose weight until they reach the average adult weight (400 grams) and fledge at between 100–110 days. Most of the weight reduction is due to the loss of water and lipids, while the amount of protein remains relatively constant (White, 1974).

Figure 25 shows growth rates and food brought to the nests of ten nestlings in four nests monitored in Guácharo Cave. There is a conspicuous positive correlation between the shape of the growth curves and the food curves. During the first twenty days the amount of food averages 68.75 grams. By the first month of development, the parents increase considerably the amount of food brought to their nestlings, raising the average to 153.75 grams. In the second month the amount of food averages 183.75 grams. After this, the parents apparently reduce the amount of food brought. This reduction is variable as may be seen when comparing nests Nos. 8 and 9 with nests No. 7 and 10. It is during this period when young Oilbirds lose weight, develop fully their primary and secondary feathers, and finally fledge.

The last nestling to hatch is outweighed considerably by its older siblings. There may be a difference of up to two weeks in hatching time in a brood of three nestlings. In Nest No. 9, an 18 gram newly hatched nestling hardly retained its weight as its older siblings, weighing 75 and 125 grams, gained weight rapidly. In this nest, as well as in nests Nos. 8 and 10, the youngest nestling eventually lost weight and died, presumably because of sibling competition or neglect by the adults.

The only nestling of Nest No. 7 stayed in the nest 76 days and finally died weighing less than 200 grams. The initial growth rate of this nestling was too slow. By the second month it weighed only 250 grams, or half that of other birds at this age. At this point the parents decreased substantially the feeding rate, promoting the starvation of their only nestling. This situation illustrates the average growth rate must be reached early during development for a nestling to obtain its asymptotic weight.

9

SEED DISPERSAL

The foraging habits of the Oilbirds may influence the dispersal of seeds of their food plants. Are Oilbirds potentially good seed dispersers? Alternatively, do they regurgitate the ingested seeds mainly in their caves? The nocturnal foraging habits along with the long distances they cover every night make it difficult to monitor what happens to the seeds once birds digest the aril of the fruits. The great volume of regurgitated seeds found in Guácharo Cave suggests that Oilbirds may be poor seed dispersers that "steal" seeds from the forest, seldom regurgitating them outside the cave.

These questions were answered through an analysis of the seeds collected in trays placed under solitary nests with various brood sizes and through the radiotelemetry data to determine the amount of time adults spent in the forest.

Assuming that Oilbird nestlings of the same age have similar feeding requirements and that all the collected seeds were regurgitated only by the nestlings, one would expect a linear relationship between the number of seeds and the brood size. In other words, two nestlings would regurgitate twice as many seeds as one nestling. If this were not the case, one would assume that any extra seeds had been regurgitated by the parents.

As may be seen in Table 13, there were conspicuous differences in the number of seeds brought to nests. Those differences were affected by brood size and length of the sampling period.

The nests were analyzed according to year, brood size, and weighed variables (seeds/day/nestling). In 1986 Nests Nos. 1, 2, and 5 showed similar values of seeds/day/nestling. The exceptions were Nests Nos. 3 and 4. The second set of nests for 1988 showed more similar values. Differences in developmental stages among nestling influenced the results. For example, the nestling from Nest No. 4 was studied during the third month of development. Nest No. 6, with no nestlings, had no seeds.

It is apparent that breeding pairs bring back to the cave mainly the fruits needed for their offspring and not for their own nourishment. Furthermore no seeds were observed in the seed traps while the birds were incubating their eggs. Additionally, radiotelemetry data showed that late in the breeding season both nonbreeding Oilbirds and breeding pairs returned to the cave only once per night (see p. 31). During the nonbreeding season the birds returned to their roosting cave after an average of ten hours of foraging activities.

It is during the breeding season, particularly the first two months of develop-

Table 13. Seed dispersal analysis.

Year	Nest No.	No. seeds	Days	Brood Size	Fruit/day/ nesting
1986	1	1901	18	1	105.61
	2	7405	32	2	102.84
	3	5000	30	2	83.33
	4	852	29	1	29.37
	5	5969	29	2	102.91
1988	6	0	20	0	0
	7	1203	21	1	57.28
	8	921	6	2	76.75
	9	1201	11	2	54.59
	10	4899	38	2	64.46

ment, when breeding pairs bring whole fruit to their offspring and also regurgitate some seeds in their cave. At this time, however, most of the seeds are regurgitated by the nestlings as suggested in Table 13.

On the conservative side, it seems that throughout the year Oilbirds might regurgitate in the forest at least 60% of the seeds collected. Additional data are needed to rigorously test this issue and determine more precisely the quantity of seeds regurgitated by adults outside their caves.

10

DISCUSSION

The nocturnal foraging movements of Oilbirds have three ecologically important aspects. First, the foraging behavior of the birds is the outcome of ecological and evolutionary pressures acting at different times during their life span. Their behavior tends to minimize predation, optimize foraging costs, and maximize reproductive success within the context of total frugivory. Second, the extreme specialization of total frugivory influences the short– and long–term foraging decisions of Oilbirds about the way they should use their habitat. Third, the role of Oilbirds as seed dispersal agents represents the bird's response to conflicting physiological and coevolutionary forces as well as plant–animal interactions. The consequences of seed dispersal by the birds are important both to the forest and to humans, and therefore to conservation efforts.

Are Oilbirds Optimal Foragers?

Conventional foraging models make specific predictions about the way birds should behave optimally. The models assume that natural selection favors traits that conform to the best fitness-related foraging strategy. Every trait correlated to foraging behavior is selected in such a way that the resulting foraging strategy, energetically or temporally, minimizes costs and maximizes benefits (Stephens and Krebs, 1986)

From the foraging movements of birds to and away from the central place, in other words the nest or roost, various quantitative approaches have been developed. The central place foraging model (Orians and Pearson, 1979; Lessells and Stephens, 1983) which focuses on individuals, predicts that the most profitable strategy for a bird carrying food for its offspring is to increase the load size and its prey selectivity (size or type of food items) as the distance from the nest increases.

Birds that fly long distances and return to their offspring with small loads would be selected against because of their reduced reproductive success. Efficient parents would tend to maximize the coefficient **E/Tt**, where **E** represents energy extracted from the prey and **Tt** indicates travel time to the foraging patch. Birds should become more prey selective as the costs associated with traveling long distances increase.

Regretably, the nature of the foraging behavior of Oilbirds restricts quantitative observations of individual intake rates, food choice, and fruit depletion rates. Thus, a rigorous test of any central place foraging model is not feasible. As a first approach to understanding the foraging ecology of Oilbirds, the utility of an optimal foraging theory, in this case refuging theory, will be evaluated while describing their foraging behavior.

Prediction 1 (p. 9) stated that Oilbirds should depart from the central place in any direction with the same probability. That prediction was supported at the colony level but not at the individual level. Individuals showed strong preferences for particular foraging patches. Since various patches occur around Guácharo Cave, the cumulative effect of the foraging directions taken by individuals generated a random pattern at the colony level (p. 23). Individual birds had the opportunity to fly to different patches, but instead they chose to forage in the same patch as long as possible. This strategy might be correlated with predictable fluctuation in the abundance and diversity of fruits within the patch.

While foraging on trees bearing ripe fruit, Guácharos might acquire information about neighboring trees, such as the presence or absence or quantity of ripe fruit; information about resources that could be readily used. The variation of fruit resources reported (p. 52) and changes in overall fruit profitability suggest that Oilbirds may exhibit some degree of fruit selectivity, although it is apparent that they capitalize on their food resources as they become available within a patch (Figs. 20-22).

The opposite strategy of visiting various localities might reduce the changes of exploiting the same tree repeatedly, although it would also increase tremendously the information about patches and trees within patches. An individual foraging for four days in a patch would lose four days of information about the status of the next location. In this scenario foraging decisions would be more complicated for individuals. A nonrandom foraging behavior, in the sense of selecting specific patches of forest without switching among patches, seems to be a good foraging strategy for Guácharos.

Many other Oilbirds were observed foraging simultaneously within the patch with a radio-tagged bird. Oilbirds definitely forage in groups at the tree level as well as at the patch level. Foraging in groups may accelerate the depletion of fruit resources. When resources eventually become scarce, intraspecific competition might increase via reduced individual intake. However, a group of Oilbirds has greater possibilities for finding ripe fruit than does an individual. In both the short– and long–term, foraging in groups might be more advantageous for the individual (Pulliam and Caraco, 1984).

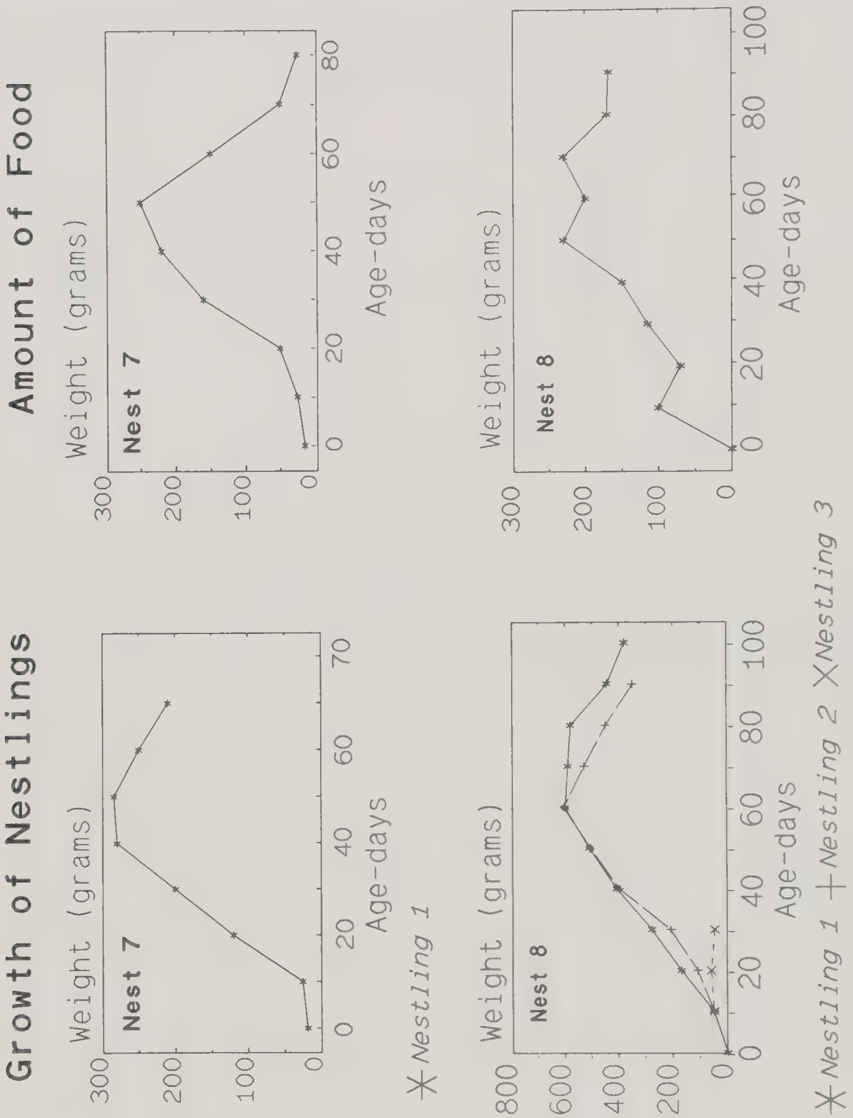
Obligate frugivory is an adaptation that exposes Oilbirds to the spatio-temporal variation of fruit resources. It may be predicted that the major proximal factor promoting long–range foraging movements is the depletion of fruit resources in the vicinity (within 20 km radius) of the central place. It was observed that Oilbirds first foraged in the vicinity of the cave and later moved to more distant patches. Their long–term fidelity (two months) to their foraging patches suggests that on a daily basis they exploit the same foraging area and probably the same fruiting trees, until food resources are diminished substantially. Fruit resources change constantly in their diversity and availability. The depletion of resources is suggested from the monthly fluctuations in dietary composition and abundance as shown (p. 98).

Oilbirds apparently minimized travel time by foraging as long as possible in the closest patches. This strategy would reduce energetic costs of travel and would increase the probability of both feeding their offspring more often and staying longer in the patch.

If intraspecific competition for fruit is the driving force promoting dispersal to remote patches, distant patches would be less intensively used than nearby patches. An inverse correlation between intensity of habitat use and distance to the foraging patches was found (p. 38). The results suggest that more remote patches were less competitive and thus potentially more valuable to birds foraging in the vicinity of the cave.

Why do Oilbirds Prefer Nearby Foraging Patches?

The progressive increase in the colony's home range represents growing travel costs, which may be considerable when visiting remote patches (Fig. 14). Since fruit availability decreases in the same months as the home range expands, breeding Oilbirds must be under strong selective pressure to minimize flying distances and to increase either the frequency of feeding trips to their nestlings or the size of the food load delivered to them. Figure 25 shows how the amount of food brought to the nestlings increased considerably as the nestlings aged. Perhaps parents progressively increased the amount of food brought to their nestlings by increasing the load size and not by increasing the frequency of trips (see p. 62). After the nestlings' second month, breeding pairs should maximize the growth rate of their nestlings in order to reach 560 grams. It appears that below average growth rates seriously impair the survival of the nestlings and, of course, the reproductive success of parents (Fig. 25). An alternative and complementary explanation is related to predation. The way to minimize predation risk is to forage away from the central place. If predation on adults were important one would expect to have found fewer foraging sites near the cave. Adult Oilbirds avoid many potential arboreal predators, such as mammals (e.g., opossums) and snakes, by flying above the forest canopy and hovering briefly to pluck off fruit. Oilbirds also fly most of the time while foraging. The major foraging concern of the birds seems to be to optimize feeding efficiency. Overall, *S. caripensis* appears to be an efficient forager. Oilbirds forage on relatively nutrient rich fruits


Growth of Nestlings
Amount of Food
Nest 7
Weight (grams)
300
200
100
0
0
20
40
60
70
Age-days
Nestling 1
Nest 7
Weight (grams)
300
200
100
0
0
20
40
60
80
Age-days
Nest 8
Weight (grams)
800
600
400
200
0
0
20
40
60
80
100
Age-days
Nestling 1
Nestling 2
Nestling 3
Nest 8
Weight (grams)
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Age-days

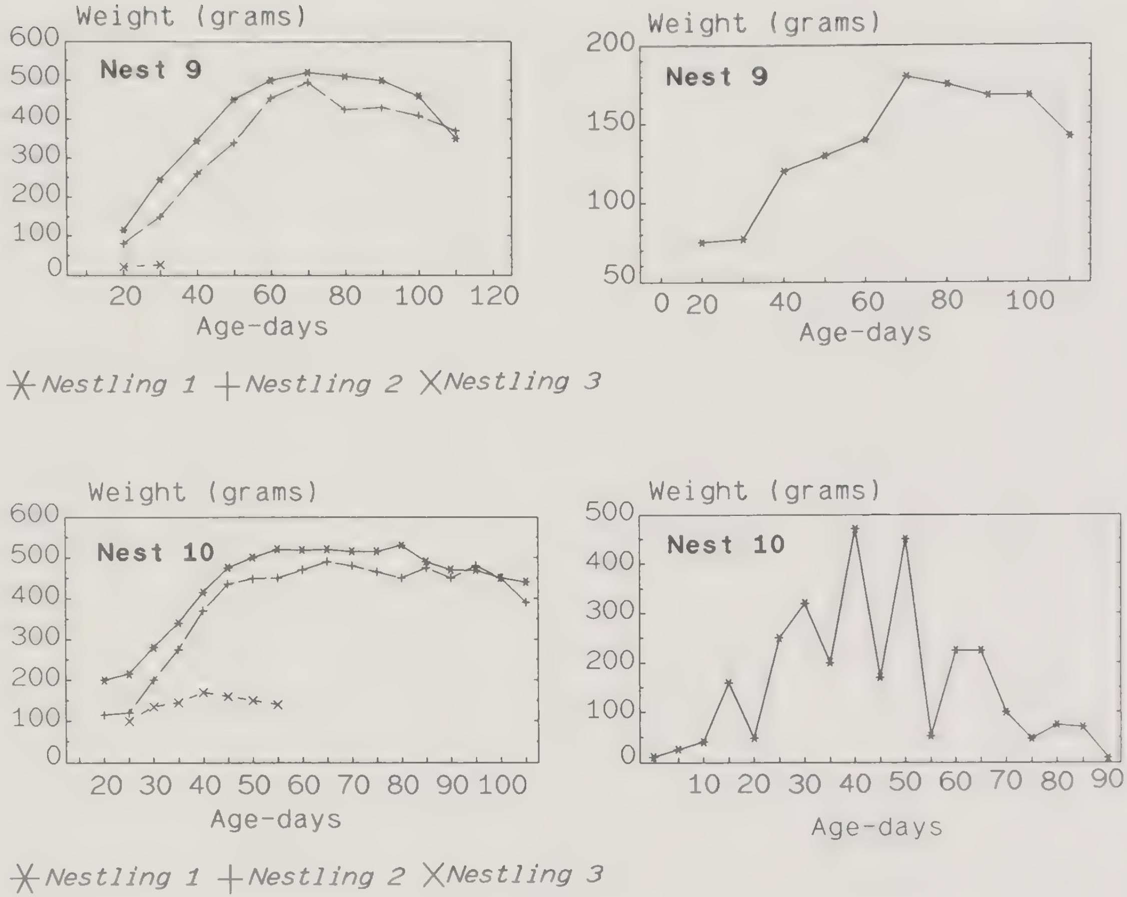

Fig. 25. Growth of nestlings and amount of food brought to Nests Nos. 7, 8, 9, and 10. The data include the entire development period until the nestlings fledge. Each point represents a single measurement per nestling.

(whether they select the most rewarding fruits remains to be determined), they forage in the closest patches first and then switch to the next closest patches, they fly straight to the patch following the same foraging routes, and they harvest fruits in a way that diminishes exposure to nocturnal predators.

Why do Oilbirds Show Postbreeding Dispersal Behavior?

Before this study it was not certain that Oilbirds indeed abandoned Guácharo Cave after they had bred. Based on two years of data, the postbreeding dispersal of Oilbirds from Guácharo Cave is now known to be a periodic phenomenon occurring at the end of each annual breeding season. This could be an adaptation to an environment with marked seasonal differences (Tannenbaum and Wrege, 1978; Snow, 1979; Bosque, 1988). In Trinidad, a less seasonal environment, fruit is produced most of the year and Oilbirds stay in their caves year around; some of them even breed twice per year (Snow, 1962).

The Oilbirds' adaptability to fluctuations in fruit resources indicates that their postbreeding dispersal behavior is triggered by a reduction in the availability of fruit. Seasonal environments definitely influence the dynamics of Oilbird populations promoting short– and long–term dispersal. Costa Rica's unique record, a desiccated corpse found in late January (Stiles and Skutch, 1989), supports the suggestion that at least some Oilbirds migrate long distances. Oilbirds apparently breed no closer to Costa Rica than Panama. How far Oilbirds disperse remains to be determined, but this study suggests that Oilbirds are long–distance migrants.

Foraging Consequences of Switching Caves and Foraging Grounds

The most striking feature of the nocturnal movements of Oilbirds is that each night some commute more than 200 km round trip to their foraging patches. Oilbirds showed unusual foraging distances after they dispersed to their new roosting caves in Mata de Mango. The distance individuals must go to reach their foraging patches is often the largest foraging cost for a refuging animal (Heithaus and Flemming, 1978). The energetic costs related to travel times to and from the patch and the benefits the birds obtain from the new set of fruit must somehow produce long–term benefits to the Oilbirds.

What fruit resources are supplying the energy needed to compensate for the high costs of traveling to the delta? Data indicate that *Jessenia bataua* is the most important fruit resource for the Oilbirds during their nonbreeding season. These palm trees, of the *Oenocarpus-Jessenia* complex, are commonly used by people throughout the northern half of lowland South American for food, fiber, shelter, fuel, and medicine. The oil contained in the mesocarp of the fruit is physically and chemically identical to olive oil (Balick, 1986). The amino acid analysis of *Jessenia bataua* protein (from the fruit pulp) when compared to the FAO/WHO provisional aminoacid scoring pattern, suggests that it is similar in quality to human milk and considerably better than most grain and legume proteins (Balick, 1986). The dry fruit pulp of *Jessenia* contains 30% lipids. A whole fruit weighs 16.25 grams and the seed constitutes 38% (6.17 grams) of the fruit (Table 11). Oilbirds ingest the whole fruit (3.2–4.0 cm long) and obtain around 2.8 grams of lipids per fruit ingested. Only 25-30 fruits per foraging trip would supply the individual's energetic demands of traveling to and from the patch, roosting in the cave all day (basal metabolism), and traveling again to the same patch the coming night.

Clearly *Jessenia*'s fruits compensate for the costs of traveling to such a remote patch and also provide Oilbirds with a high quality source of protein. The disadvantage of foraging on such a large fruit is the ballast or extra weight due to the seed. Guácharos must regurgitate the large seeds as fast as possible to both increase their intake rate and decrease the extra load before returning to their caves. The small number of *Jessenia* seeds found in Guácharo Cave (see Table 7) supports the idea.

Developmental Implications of Total Frugivory

Predation in Guácharo Cave is restricted to nests built on accessible ledges where rodents such as *Proechymis urichi* steal eggs from Oilbird nests (Ramírez, 1987). I have also seen rats preying on small nestlings that fall from their nests. Many nesting ledges, within galleries in the cave ceiling and other inaccessible places, are free from predation. Reduced predation has promoted a long development period for Oilbirds and has played an important role in their totally frugivorous diet (Morton, 1973).

Oilbird nestlings are fed on nutrient– and lipid–rich fruits. In the first month of development the daily rate (grams/day) of gained proteins and lipids have a 1:2 ratio respectively. The ratio changes to 1:3 the second month (White, 1974). Thus, during the long development period there is an increasing amount of extra lipids per each gram of protein incorporated in the tissues. The nestlings have two physiological options: they could either metabolize the excess lipids, or they could store them in fat cells. Metabolizing the excess lipids would mean activity for the nestlings, and this option would take time.

Storing extra lipids in fat cells makes more sense in a seasonal environment where fruits are available for a limited time. For the Oilbirds it is more advantageous to process nutrients quickly by storing fats rather than by metabolizing lipids for a day or two. Since fruit production fluctuates within a season, taking the time to metabolize the fats might lead to a deficit of nutrients by the second month. At this time it would be difficult for the parents to compensate for the deficit because of the reduced availability of fruit. Storing fats, on the other hand, has the additional advantage of temporarily compensating for any reduction in the amount of fruit brought to the nest. The excess fat is also used later, the third month, after the parents cease feeding their nestlings.

Bosque and Parra (1992) reported that Oilbird nestlings extracted an average of 88% of dietary nitrogen from an avocado-based diet. Oilbird nestlings apparently maximize their efficiency in converting dietary protein to tissue. This adaptation implies that Oilbird nestlings allocate a small percentage of nitrogen to maintenance in comparison to that used to build new tissue. The study also found that the digestibility of fat (80%) was also relatively high. Oilbirds seem to use the fat as fuel to supply metabolic demands related to maintenance, feather, growth, and muscle development.

In summary, total frugivory by Oilbirds seems to be the result of a relatively predation–free niche that does not constrict the nesting period. The exaggerated weight gained by the nestlings appears to be the outcome of multiple ecological and physiological forces promoting fat storage as an optimal strategy.

11

CONSERVATION

In recent decades our biosphere has experienced unprecedented changes because of human–induced disturbances (e.g., ozone depletion, greenhouse effect, air, water and soil pollution, tropical and temperate forest destruction, extinction of species, etc.). These changes have affected biodiversity negatively at all levels from the gene pool to species and the natural community.

Preserving biodiversity is one of the most revolutionary and adaptive responses we have developed during the process of our cultural evolution. New concepts and changes in our society are not readily incorporated, and for that reason the community of scientists must take the lead proposing adequate ways to achieve the goal of conserving our natural heritage.

Each year more than 20.4 million ha of tropical habitats are destroyed (World Resources Institute, 1990). The rate of biological extinction is the highest in human history (Wilson, 1988). Because of this, any regional or even local effort to preserve our natural heritage is meaningful. In Venezuela various nongovernmental organizations as well as the Ministerio de los Recursos Naturales Renovables (MARNR) have taken responsibility for monitoring and preserving natural resources of that country.

Proposed Extension of Guácharo National Park

In 1989 it was proposed to MARNR that Guácharo National Park be enlarged (Roca and Gutiérrez, 1989). The central objective of the proposal was to include the karst zone of Mata de Mango. The annexing of this area to the existing park would guarantee not only the protection of food and cavern resources for the Oilbird colonies inhabiting the region, but also the protection of a complex hydrological network that supplies water to the local agricultural and oil activities.

For South America the conservation aspect of this research on Oilbirds constitutes a novel scientific approach for supporting the preservation of tropical forests.

The central theme of the proposal was based on the information that Oilbirds forage only within about 25% of the then-existing area of Guácharo National Park. Most of the colony forages outside the confines of the park, preferring remote patches of primary forest and avoiding disturbed areas. Foraging by the colony follows the distribution of resources. Resources are more abundant toward the southeast in Mata de Mango, the new area proposed to be included in Guácharo Park. Each year after breeding the colony migrates to the caverns present in Mata de Mango (p. 41) and forages mainly toward the floodplains of the Orinoco Delta. Ideally, the proposal should have incorporated within the protected area the floodplains, because these are part of the foraging grounds of the colony, but for practical reasons this vast area was omitted. However, MARNR and INPARQUES currently are assessing the floodplains for future protection. The Orinoco Delta is also a valuable habitat for the manatee; it is important to fisheries and aquiculture; and it is the natural territory of various Amerindian tribes.

Ecological and Conservational Importance of Oilbirds

The Oilbird's ecological attributes highlight the role of the species in the ecosystem. Its annual breeding cycle, long lifespan, short– and long–range foraging movements, large home range, postbreeding dispersal, broad diet, high density, and its function as a good seed dispersal agent, make it a keystone species for the tropical forest.

The highland and lowland forests benefit from having Guácharo–disseminated seeds throughout the a vast area that encompasses various plant communities. I have calculated a conservative estimate of the magnitude of this bird`s seed dispersal. An adult Oilbird needs an average of 50 fruits per day to supply its daily metabolic demand, using Nagy's (1987) field metabolic rate equation and my own calorimetry data. An individual bird regurgitates 1,500 fruits monthly and the entire Guácharo colony regurgitates 15,000,000 seeds monthly. That represents a biomass of about 21 tons of seeds, excluding the aril, that are regurgitated each month by the entire colony. Whether adults disperse all the seeds or only a fraction remains to be determined. My results suggest that Oilbirds regurgitate seeds in the forest during both the breeding and nonbreeding season. Overall at least 60% of the seeds are dispersed in the forest (p. 64).

Several aspects of the natural history of Oilbirds are important to their conservation, viz., their colonial cave-dwelling habits, the long development of their nestlings, their total dependence upon primary forest resources, and their vulnerability to human activities (predation and habitat loss). Oilbirds constitute an excellent ally of mankind in the hard task of preserving wildlife areas. Oilbirds could be considered as a natural tool for management of regions, like Mata de Mango, that require special protection. Through their seed dispersal role, Oilbirds may contribute to the maintenance of plant diversity of the watersheds.

Limestone formations are particularly sensitive to erosion, and plant cover is the only way these geological processes are slowed. Any major element of the ecosystem that supports the forest structure, in this case Oilbirds, is important and must be protected.

Ecological Value of Mata de Mango

Mata de Mango encompasses 34% (18) of all the Oilbird colonies reported for Venezuela (Bosque, 1986). Other colonies are scattered through the country. This area is probably the most important habitat for the species within its range.

Mata de Mango is also a natural refuge for the flora and fauna of the northeastern part of the mountain range. The area is like a "mountainous island" surrounded by small farming villages. Unfortunately, the size of the "island" is being reduced because of the slash-and-burn techniques practiced by the growing number of farmers (*conqueros*) in the area. Their activities not only threaten the fauna and flora but also undermine the fragile hydric network of the Caripe region. The *conqueros* are catalyzing the sedimentation and erosion processes that normally should take thousands of years. Mata de Mango embraces 33 headwaters of a lowland river, the Río San Juan. Most of the San Juan waters are navigable. The river flows into the Golfo de Cariaco. Its characteristics make the San Juan the route of fisherman and large oil tankers coming to the town of Caripito on the upper part of the river. The erosion and sedimentation of the hydric network of the highlands would negatively affect the main economic activities of the area and would have a major impact on the farms in the vicinity of Mata de Mango.

The proposed enlargement of the existing park did not pretend to serve to preserve the flora and fauna per se, and would not stop development projects of the state of Monagas. The enlarged park would complement and guarantee a sustainable development process in harmony with the natural environment.

Relevance of Proposal

Guácharo Cave was declared a natural monument in 1949. Guácharo National Park was created in 1975 to protect both a local watershed and the foraging grounds of the Oilbirds, but at the time there was little information about the foraging ecology of the Oilbirds (Tannenbaum and Wrege, 1978, 1984). The present investigation showed that the initial dimensions of the park were not large enough to guarantee the long-term survival of the Guácharo colony inhabiting Guácharo Cave (Roca and Gutiérrez, 1991).

The proposed new area of Guácharo park is relatively close to Guácharo Cave and has large amounts of primary forest. The forests adjacent to the park still provide fruit for the colony but these forests were being quickly destroyed because of the unselective slash-and-burn technique practiced in the region.

Annual summer fires are typical in the Caripe valley. These fires destroy hundreds of hectares of forest and are the major threat to the Guácharo colony. In a few years Oilbird numbers might be reduced considerably; eventually the colony might either migrate to a more suitable habitat or go extinct.

From all the possible areas of expansion near Guácharo Cave, Mata de Mango was the most suitable. If Mata de Mango could be actively protected, Oilbirds would have a permanent sources of good food and caverns.

Annexing the Area

Because the new area is about 15 km from the park, two methods of expansion were evaluated. First, connecting both areas through a natural corridor, or "greenway". Through this method the park would not have been fragmented and some fauna, mainly mammals and birds, could have used the corridor. The second possibility was that both areas would be separate but close enough for birds to commute. The first alternative would have given unity to the park and could have been more beneficial for the flora and fauna as a whole, but in reality management of any land takes into account nonbiological information. For

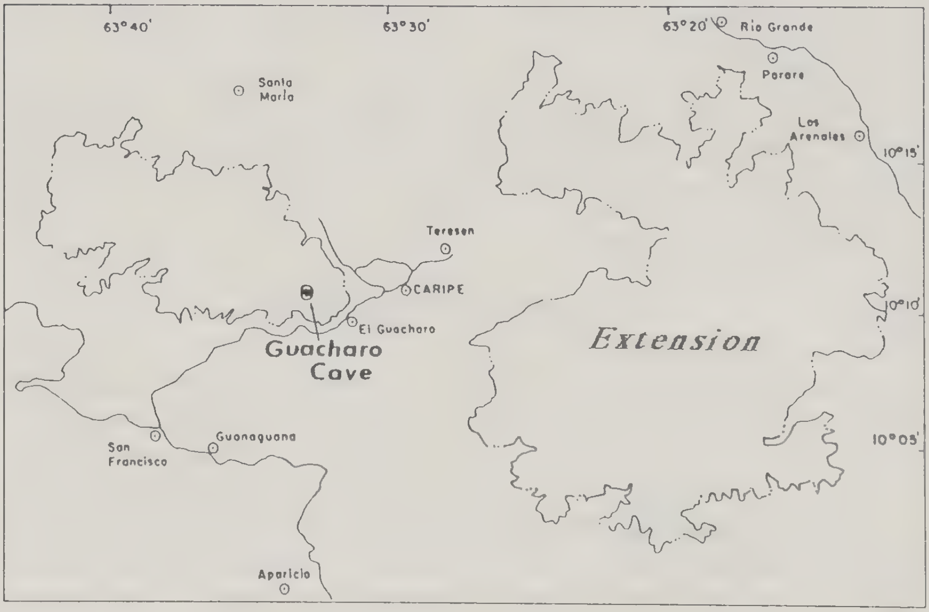

Fig. 26. Enlargement of Guácharo National Park.

example, the landowners, the number of private properties and their size, the location of villages, agricultural zones, and state-owned lands are all important. The final success of a proposal depends on its feasibility.

An adequate natural corridor was difficult to devise. Most of the land between Guácharo Park and Mata de Mango is heavily populated. The town of Caripe and various small villages and coffee and orange plantations along the Caripe valley posed numerous administrative and legal hindrances to the establishment of the corridor. The second alternative was more expedient.

The borders and size of the new area (Fig. 26) were delimited following four major criteria:

1. All the caverns and sinkholes within the area were included.

2. A large patch (66,400 ha) of mainly primary forest, similar to the home-range size of the colony, was included.

3. All 33 headwaters of the Río San Juan were included.

4. Most of the towns, small villages, farms and private lands were excluded.

The second design was accepted without major changes by MARNR and INPARQUES.

The proposal was supported and accepted because of the cooperative effort of numerous agencies and organizations, viz., MARNR, INPARQUES, Fundación para la Defensa de la Naturaleza (FUDENA), International Programs of NYZS/ Wildlife Conservation Society, BirdLife International, and the State University of New York at Albany (SUNYA).

On 13 December 1989 the then minister for the environment, Enrique Colmenares Finol, officially declared the extension of the Guácharo National Park by 66,000 ha.

The new and expanded "Guácharo National Park" is now a reality.

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